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BULLETIN OF THE TORREY BOTANICAL CLUB
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INHERITANCE OF ORANGE AND YELLOW FLOWER COLOR IN NEMESIA STRUMOSA

HERBERT PARKES RILEY

In 1929 the author undertook to study the interaction of the genes that produce the many different flower colors in *Nemesia strumosa*. This work was carried on until 1932 as a graduate student in Dr. Geo. H. Shull's laboratory at Princeton University and was continued for the next two years as a National Research Council fellow in the biological sciences at the Bussey Institution of Harvard University under the late Dr. E. M. East. By 1934, seventeen genes for flower color had been identified at least tentatively, and a report showing that self-sterility is determined by oppositional factors was published the following year (Riley 1935). The results of the study of the inheritance of flower color were not published at that time, however, because it was considered desirable to investigate several points more thoroughly and to check more carefully several possible linkage relationships. An abstract describing briefly five of the genes was published in 1940 and one showing that two flower color genes are linked with the self-sterility alleles was published in 1944.

Nemesia strumosa Benth. is a South African plant of the Scrophulariaceae which has been in cultivation in this country since the last part of the nineteenth century (Bailey 1937). Although Bailey states that this species is of easy cultivation, the author has found that this is true only within certain limits. Most of the plants used for this study were grown in the greenhouse during the winter. In general they grew very well, but on some occasions they appeared highly susceptible to certain fungi, and in each of two years several hundred plants were lost before flowering because of an attack of *Botrytis cinerea*. During another year, a large number of plants was lost when the greenhouse was fumigated with formaldehyde. Some plants were grown out-of-doors but this species frequently does not stand the summer heat in New Jersey or New England very well, and Taylor's (1936) statement that it is "essential for them to make as much growth as possible before summer heat" is appropriate.

After carrying on this study for several years, the author moved to a location where he had no facilities for growing plants during the winter months and where the summer climate was too hot for Nemesias. After several attempts to continue this problem, it was given up. Four years later, he again moved to a more suitable location and attempted to resume these studies. During three successive years, the seeds of a number of the old

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pedigrees were sown in a greenhouse in the usual manner but apparently the delay had been too long, for not one seed had remained viable. The author then obtained new lots of seeds and has continued the study with these new plants; but unfortunately, several of the old flower-color types have not been secured as yet in the new material.

MATERIALS AND METHODS

The original plants were grown from a seed packet purchased from Peter Henderson and Co. in New York in 1929 and labelled, "Nemesia—Newton's Glories mixed." Twelve plants were selected for the original crosses, and all families of the earlier part of this study were descendants of these plants. These twelve plants were apparently heterozygous for a great many genes, for 75 different phenotypes were described and catalogued from the F_1 generation of 13 crosses among these original plants. Subsequently, it was found that a few of these 75 phenotypes were fluctuations and that some others were the result of modifying genes of slight effect which could not be readily analyzed, but most of these types represented genes or combinations of genes which could be at least partially analyzed. The original plants were photographed in color on lantern slides, while later generations were recorded in water color and by descriptions based on a comparison with Ridgway's (1912) color charts. With a few exceptions, all crosses were guarded and the usual precautions of the pedigree culture method were observed.

After it was learned that seed from the original lines was no longer viable, a number of new lots of seeds were purchased and sown. In 1940, packets of seeds of *N. strumosa Suttoni* including "Blue," "Orange," "Pink," "Scarlet," "White," "Yellow," and "Mixed Colors" were purchased from Peter Henderson and Co., while packets of *N. grandiflora Suttoni* mixed, of *N. compacta* (= *N. versicolor*) "Triumph," and of *N. compacta* "Blue Gem" were purchased from the Ferry-Morse Seed Co. In 1943, new lots of "Blue," "Orange," "Pink," "Scarlet," "White," and "Mixed Colors" of *N. strumosa Suttoni* were obtained from Peter Henderson and Co., while lots of *N. strumosa* "Tall Blue," and of *N. compacta* "Fire King" were purchased from Herbst Bros. in New York.

The flower of *Nemesia strumosa* has a corolla with a short tube which bears a short spur or pouch. The limb of the corolla is two-lipped and the upper or posterior lip is strongly notched so that it has four distinct parts. The lower or anterior lip usually has one shallow notch in the center. There are four didynamous stamens which usually cohere about the stigma (fig. 1). The corolla limb on the inside may be white, orange, yellow, or several shades of red and purple; there may be a blue margin on the upper lip, or it may be spotted or streaked with red. The lower part of the tube may be

orange or straw-color and may have a few or many dots of very deep purple. The upper part of the tube is generally colorless, but above the stamens there frequently is formed a large spot of very deep purple, which the author calls the "eyebrow." Apparently these colors all exist in wild plants (Bailey 1937), and apparently a very large number of interacting genes is present.

A genetic analysis of this species is rendered somewhat difficult by the fact that it is self-sterile (self-incompatible). Because of the presence of self-sterility alleles, it is impossible to obtain seed by self-fertilizing mature flowers, and it is sometimes impossible to make certain crosses because the plants to be crossed have the same self-sterility alleles. All families, therefore, arose from sib crosses or from crosses between plants of two different families. When dealing with a typical heterozygous F_1 generation it makes

FIGS. 1–3. Diagrams of flowers of *Nemesia strumosa*. Each flower is cut along both sides of the tube and is then flattened out. This causes some distortion of the tube but little distortion of the lips. FIG. 1. The white-flowered, standard type. FIG. 2. Orange; the shaded areas show the distribution of the orange pigment in the lips. FIG. 3. Yellow spot; the approximate distribution of the pale yellow pigment on the lower lip is indicated by the dark spot and radiating lines.

no difference whether an F_2 generation is produced from it by the self-fertilization of one plant or by a cross between two sibs. However, this is not the case when seeds from other than typical F_1 generations are desired, for in such families plants that are alike phenotypically do not necessarily have the same genotype. This is an important consideration in this *Nemesia* study, for the original plants were mostly heterozygous for a large number of the genes and the families which arose from crosses among them were therefore not typical heterozygous F_1 families. Since it was impossible to self-fertilize individual plants, subsequent generations had to be produced by crossing two plants, and there was no assurance that two plants were alike genotypically even though they were sibs and were alike phenotypically. For example, in several instances it was desired to determine whether the offspring of a dominant type would segregate into a 3:1 or some other ratio. If the family to be tested were from seeds of unknown ancestry, it is possible that

some of the dominants might be homozygous; if the species is self-fertile, the chance of securing a heterozygote for breeding by self-fertilization would be only two in three plants. When the species is self-sterile, segregation of the offspring will be obtained only when two heterozygotes are crossed. In a family segregating in a 3:1 ratio, the chance of obtaining two heterozygotes simultaneously is only four out of nine, which shows that the chances of a successful test, when the original parents are not homozygous, is considerably less in a self-sterile species than in a self-fertile one.

A further complication arises if some of the genes to be tested happen to be linked with the self-sterility alleles for, in self-sterile species, genes which determine morphological characters do not give typical mendelian ratios in certain crosses if they are linked with the self-sterility alleles. In 1926, Brieger and Mangelsdorf showed that the basic color gene *C* in *Nicotiana* is so linked; and Williams (1935, 1937) subsequently showed that five genes in red clover are on chromosome-II in addition to the self-sterility alleles. Anderson and De Winton (1931) found that in hybrids of *Nicotiana Langsdorffii* and *N. alata* at least one gene for corolla-tube length is linked with the self-sterility alleles. They found also that at least one of the several pairs of genes that determine differences in the proportionate length of the style in *Nicotiana* and one of the pairs of alleles that determine pollen color in crosses between *N. Langsdorffii* and *N. alata* appear to be strongly linked with the self-sterility alleles.

Linkage with self-sterility genes is important because of gametic elimination in certain crosses. If two plants are mated that have no self-sterility allele in common, as in the cross $s^1s^2 \times s^3s^4$,[1] there will be no gametic elimination; if each of these plants is also heterozygous for a gene determining some morphological character, the offspring will segregate in a monohybrid ratio for that character whether or not the self-sterility alleles and this other gene are linked. If, on the other hand, the two plants have one self-sterility allele in common, the result will be different. If there is complete linkage, and if the dominant morphological gene of the male parent is on the same chromosome as the common self-sterility allele, the offspring will segregate into a ratio of one dominant to one recessive. Such a cross is $s^1A/s^2a \times s^1A/s^3a$. Because of the elimination of the s^1 pollen, the two resulting types of offspring will be s^1A/s^3a and s^2a/s^3a. If linkage is not complete, the ratio will be less than 3:1 but greater than 1:1, and there will be an excess of recessives. If the recessive morphological gene in the male is coupled with the common self-sterility allele and if linkage is not complete, there will be an excess of dominants, as in the cross $s^1A/s^2a \times s^1a/s^3A$.

In backcrosses in which there is linkage between the genes for self-steril-

[1] Superscripts rather than subscripts are used in this paper to designate self-sterility alleles. See de Haan (1932) and Riley (1932).

ity and those for morphological characters, reciprocal crosses do not always give the same results. If a homozygous recessive female is crossed with a heterozygous male in which the dominant gene is coupled with the common self-sterility allele, there will be an excess of recessives in the offspring. In the cross, $s^1a/s^2a \times a^1a/s^3A$, there will be an excess of dominants. In each case, the reciprocal cross will yield a ratio of one dominant to one recessive.

OBSERVATIONS

White. In the white-flowered plants, the inner parts of both lips of the corolla are white, while the lower part of the tube is Orange[2] or Orange Chrome. Deep purple spots may be present or absent on the lower part of the tube and the "eyebrow" may or may not be present. The cells of the corolla lips are mostly papillate and there are few, if any, hairs. In the lower part of the tube, the papillae are longer than in the cells of the lips. Almost all the cells of the lower part of the tube appear to be completely filled with deep yellow pigment. When examined microscopically, the papillae of the cells seem to be of a deeper color than are the remaining parts of the cells, but this probably is merely the result of a greater thickness of the cell at that place. When white flowers are placed in ammonia vapor, the corolla lips begin to turn yellow at once. When the color change has been completed, they are Lemon Yellow, and all the epidermal cells when examined under the microscope are yellow. The orange tube does not change color. In hydrochloric acid vapor, the lips become Orange-Buff on the inside, but in dilute nitric acid they appear to remain unchanged.

The white-flowered type will hereafter be regarded as the standard type. This is not to be understood as a wild-type in the sense in which the word is applied in *Drosophila*, for many of the other types occur frequently in nature and some perhaps as frequently as does the white-flowered type. This type, however, will be used as a type of reference or a standard from which other types will be regarded as departures or mutants.

Orange (*O*). Like the white-flowered plants, the orange-flowered type is common. The "orange" color is probably very deep yellow (fig. 2) rather than orange, and may be lightened in color by at least two principal modifying genes in addition to others of small effect.[3]

In orange-flowered plants that are not affected by these principal modifying genes, the lips are usually either Light Cadmium or Cadmium Yellow, although in a few plants the color seems close to Orange. The orange color is

[2] Colors are capitalized which are standardized from Ridgway (1912).

[3] In a preliminary report (Riley 1940), the author called this type yellow and used the symbol *Y* to designate the dominant gene for this color. He has learned subsequently, however, that this type is sold commercially as orange rather than yellow. In order to conform to that practice, he will designate this type as orange hereafter and will substitute the symbol *O* for the *Y* of the preliminary paper.

confined to the epidermal cells. These cells are papillate and the water-soluble orange pigment appears to fill the whole cell. The tube is the same as that of the white-flowered type. When placed in ammonia vapor, there is no change in either the lips or the tube. When the orange-colored epidermis is stripped off, however, exposing the colorless subepidermal layers, the exposed portions turn Lemon Yellow. In HCl vapor, the orange color of the lips and tube becomes paler and in some cases fades out almost entirely. In sulfur dioxide the lips remain unchanged and the orange color of the tube becomes very slightly paler.

Orange behaves as a simple dominant over white. In 16 families which resulted from a cross between two orange types, 377 orange and one white plant were produced. It is not unlikely that the white was an interloper. In 12 of these 16 families, one or both parents contained anthocyanin pigment in addition to the orange pigment, but in tabulating the ratio of orange to white, only plants lacking anthocyanin were included. Twenty-eight families were the result of crosses between two non-orange plants one or both of which may also have contained an anthocyanin pigment. The offspring that did not contain anthocyanin included 759 white-flowered but no orange-flowered plants. Crosses between apparently homozygous orange and non-orange plants produced seven families which contained 443 orange and one white-flowered plants, not including those with anthocyanin. Again, this lone white plant may have been an interloper.

That orange is dominant is shown by the fact that in seven families of different parentage, orange × non-orange gave orange. It was desirable to confirm the dominance of orange by crossing two heterozygotes but this test was not set up until 1933 and it was not possible to raise the seeds from those crosses. Seven families from crosses between orange and non-orange yielded a total of 104 orange- and 104 white-flowered plants. In no family was the deviation as great as twice the standard error. The symbol for orange will be *O*.

Linkage between the orange gene and the self-sterility alleles has not been tested, since the self-sterility alleles of one parent in five of these test-crosses was unknown, while in the other two crosses, the self-sterility groups of both parents were undetermined.

Pale-upper (*p*). This type appears to be a modification of orange and has several expressions depending, perhaps, upon other genes. Typically, the lower lip is Light Cadmium and the upper lip is Apricot Yellow or Empire Yellow, or between them in color. In some plants that appear to be genetically similar to the typical form, both lips are Light Cadmium, but this deep yellow color of the upper lips is largely restricted to the central part of the lobes and almost completely fades out at the edges. In some plants, the upper lips are Maize Yellow with some spots of Buff Yellow or of Light Cadmium

on the inner parts. The lower part of the tube is Orange, as in the white and orange types, and may or may not have deep purple spots. The gene for pale-upper seems to affect only gene *O*, for pale-upper and non-pale-upper cannot be differentiated in *oo* plants. In one cross, a white plant was crossed with a pale-upper which was heterozygous for *O*. The offspring segregated into 14 deep orange : 11 pale-upper (orange) : 30 white. The appearance of the deep orange type from a white × pale-upper cross indicates that white and pale-upper do not differ by just a single pair of genes.

That pale-upper is recessive to orange is shown in a number of cases. Eight families resulting from a cross between two plants apparently heterozygous for pale-upper and of which at least one was *OO* segregated into 285 orange and 110 pale-upper against an expected ratio of 296 : 99. In no family was the deviation more than twice the standard error. Nine families

TABLE 1. *Observed ratios of orange (non-pale-upper) to pale-upper in eight families in which one self-sterility allele was common to the two parents, and the corresponding expected ratios based on the absence of linkage between the pale upper gene and the self-sterility alleles.*

Family	Parents	Genotypes of parents	Observed		Expected		Dev./S.E.
			P	*p*	*P*	*p*	
3103	3001(6) × (22)	$s^2s^3pp \times s^3s^2Pp$	13	8	10.5	10.5	1.09
3105	3001(8) × (22)	$s^2s^3pp \times s^3s^2Pp$	10	0	5.0	5.0	3.10
3225	3103(1) × (5)	$s^3s^2pp \times s^2s^2Pp$	7	9	8.0	8.0	0.50
3223	3103(3) × (52)	$s^3s^2Pp \times s^2s^2Pp$	16	9	18.8	6.2	1.30
3226	3103(5) × (3)	$s^2s^2Pp \times s^3s^2Pp$	20	2	16.5	5.5	1.72
3361	3103(52) × (4)	$s^2s^2Pp \times s^3s^2Pp$	7	0	5.2	1.8	1.55
3362	3103(52) × (40)	$s^2s^2Pp \times s^3s^2Pp$	26	10	27.0	9.0	0.38
3411	3103(4) × (52)	$s^3s^2Pp \times s^2s^2Pp$	5	3	6.0	2.0	0.82

resulted from crosses between a heterozygote and a pale-upper plant. While the total consisted of 114 orange and 78 pale-upper, in only one of the families did the ratio of the deviation to the standard error exceed 2, and in this family the number of individuals was small. It seems reasonably certain that pale-upper is recessive to orange; the symbol *p* will be used to designate this gene.

Evidence on linkage between the pale-upper gene and the self-sterility alleles is not so abundant as might be desired, but the data that are available indicate that there is no linkage. In three test-crosses in which the parents had a common self-sterility allele and the male parent was heterozygous for *P*, only one family showed a ratio of which the deviation was more than twice as great as the standard error (table 1). In five families in which both the parents were heterozygous for *P* and had one self-sterility allele in common, the deviation was less than twice the standard error. These eight families do not indicate any linkage relationship between pale-upper and self-sterility.

Little evidence is available to indicate whether *o* and *p* are linked, but what evidence there is is negative. Two families resulted from the cross *OoPp* × *ooPp*. Since *P* and *p* cannot be differentiated in the *oo* plants, the test for linkage is whether the orange and pale-upper types segregate into a 3 : 1 ratio. In these families the ratios were 7 : 2 and 21 : 5. Since neither differs significantly from a 3 : 1 ratio, there is some evidence that *o* and *p* are not linked.

Buff (*bu*). Like pale-upper, buff appears to be a modification of orange and is rather variable in expression. Most typically, the lower lip of the corolla is Light Cadmium near the throat, but most of the lip is Buff Yellow and the edges may be as light as Sulphur Yellow; the upper lip is Sulphur Yellow with areas of Buff Yellow. In some plants of the buff type, the paler regions of the lips are Baryta Yellow, and the deeper places are Empire Yellow. The lower part of the tube is Orange and may or may not have deep purple spots. Buff gives the general appearance of being much paler than pale-upper.

Buff is a modification of orange, and is not expressed in *oo* plants. In plants with the *O* gene, buff appears to be recessive to non-buff. In a number of crosses between two non-buff plants, only non-buff offspring appeared, while in one cross between two buffs there were 27 buff and no non-buffs. Four families arose from a cross between two heterozygotes and produced a total of 122 orange (non-buff) : 54 buff, and in no family was the deviation twice as great as the standard error (table 2). In three backcrosses of a non-buff to a buff, the ratio was 18 non-buff : 23 buff, and in no family did the ratio of the deviation to the standard error exceed 2. That buff and white are not the result of allelic genes is shown from two families in which a white that apparently was homozygous for non-buff was crossed with a buff heterozygous for *O*. In one family, the ratio was 26 orange (non-buff) : 17 white, while in the other family it was 9 orange (non-buff) : 12 white. If white and buff differed merely by a single gene, orange-flowered (non-buff) plants would not have been recovered from a white × buff cross. Buff, then, is apparently recessive to non-buff and is independent of gene *O*. The gene for buff will be designated by the symbol *bu*.

Four other families arose from crosses between two *Bu bu* plants but each exhibited a very poor fit to a 3 : 1 ratio (table 3). If, however, the buff gene is linked with the self-sterility alleles with about 5 per cent crossing over, the observed ratios are much closer to the expected. If family 3103 arose from the cross $s^x bu/s^y Bu \times s^y Bu/s^z bu$, the s^y male gametes would be eliminated. Except for crossing over, these would also be *Bu* gametes, so the expected ratio would be close to 1 : 1 with a slight excess of non-buff plants due to crossing over. The observed ratio was 21 non-buff : 23 buff which is much closer to the expected ratio based on linkage than to that based on no linkage.

Families 3104, 3105, and 3106 arose from similar crosses in which the *Bu* gametes were eliminated in the male except for those that arose by crossing over. While these families are rather small, they deviate much less from the expected ratios based on linkage with the self-sterility alleles than they do from the expected 3 : 1 ratios.

Three families arose from backcrosses of a heterozygous male to a recessive female. In each case, the observed ratio was not even close to a 1 : 1 ratio. All three families appear to arise from crosses in which the *bu* gene is linked with the common self-sterility allele in the male, for in all cases there is a great excess of dominants in the offspring. In families 3225 and 3361, the numbers are small and there are no recessives, but in family 3362, in which the numbers are larger, there are a few recessives, which undoubtedly represent crossovers.

Whenever disturbed ratios appear, an explanation must be sought, and an explanation that has often been suggested is selective fertilization. In a number of cases it has been shown that this is due to a difference in the growth rate of pollen tubes so that tubes of a given genetic constitution will grow more rapidly or more slowly than those whose genetic constitution is somewhat different. Several discussions of various types of genes for differential pollen tube growth have been recorded, (Brieger 1926, Sansome & Philp 1932, Sears 1937), and Mangelsdorf and Jones (1926) have pointed out that genes affecting the rate of pollen tube growth may be of four types: (1) those which reduce growth rate in sporophytic tissue of the same genetic constitution (self-sterility alleles); (2) those which reduce the rate regardless of the genetic constitution of the sporophytic tissue; (3) those which stimulate the rate in sporophytic tissue of the same genetic constitution; and (4) those which stimulate the rate regardless of the genetic constitution of the sporophytic tissue.

If differential pollen tube growth is considered as a possible explanation of disturbed ratios, the various types of pollen tube growth-rate genes must be considered, for the fact that the ratios of non-buff to buff are in accord with an explanation based on linkage with self-sterility alleles does not, of course, preclude that some other explanation might fit the facts just as well. If pollen tube growth-rate genes are believed to be the cause of these disturbed ratios, it is simpler to assume that the buff gene is linked with the self-sterility alleles than to hypothesize an additional set of genes which affect pollen tube growth-rate; still, it may be helpful to consider briefly the possibility of linkage with some other type of gametophyte gene, perhaps similar to the *Ga* gene of Mangelsdorf and Jones. For example, while families 3103, 3104, 3105, and 3106 agree well with the concept of linkage with self-sterility gene with 5 per cent crossing over, they will also agree just as well with a theory based upon linkage of *bu* with gametophyte genes

TABLE 2. *Observed ratios of orange (non-buff) to buff in seven families of which the parents possessed no self-sterility allele in common, and the corresponding expected ratios.*

In the first four families, each parent was heterozygous for the buff gene. In the other three, one parent was *bu bu*.

Family	Parents	Observed		Expected		Dev./S.E.
		Bu	*bu*	*Bu*	*bu*	
3001	2901(1) × (7)	11	6	12.8	4.2	1.01
3002	2901(1) × (11)	37	18	41.2	13.8	1.30
3003	2901(1) × (15)	61	27	66.0	22.0	1.23
3015	2901(14) × (1)	13	3	12.0	4.0	0.58
3004	2901(7) × (13)	6	4	5.0	5.0	0.63
3006	2901(9) × (10)	9	13	11.0	11.0	0.85
3009	2901(10) × (5)	3	6	4.5	4.5	1.00

such as *Ga* with 5 per cent crossing over, provided that *Ga* is not merely 4.1 times as successful as is *ga*, as Mangelsdorf and Jones found in maize, but that it is completely successful. Such a theory is very similar to that based on linkage with the *s* genes, except that there should be no correlation between families with disturbed ratios and families whose parents had a self-sterility allele in common. Table 2 lists seven families whose parents did not have a common self-sterility allele, and in all these families the non-buff : buff ratios cannot be regarded as disturbed. On the other hand, the seven families listed in table 3 have parents that shared one self-sterility allele, and they do have disturbed ratios. Family 3001 had parents with no common allele, and conforms sufficiently well to a 3 : 1 ratio, but four of its F_1 descendants had parents with a common allele and definitely showed disturbed ratios. This would indicate linkage with the *s* genes rather than with *Ga* genes.

TABLE 3. *Observed ratios of orange (non-buff) to buff in seven families of which the parents possessed a common self-sterility allele, and the corresponding expected ratios based on absence of linkage between the buff gene and the self-sterility alleles and on linkage with five per cent crossing over.*

In the first four families, each parent was heterozygous for the buff gene and *Bu* is coupled with the common self-sterility allele in the male. In the other four, the female parent was *bu bu*, and *bu* is coupled with the common *s* allele in the male.

Family	Parents	Observed		Expected					
				If no linkage			If linkage		
		Bu	*bu*	*Bu*	*bu*	Dev./S.E.	*Bu*	*bu*	Dev./S.E.
3103	3001(6) × (22)	21	23	33.0	11.0	4.18	23.1	20.9	0.63
3104	3001(22) × (6)	3	3	4.5	1.5	1.42	3.2	2.8	0.16
3105	3001(8) × (22)	10	10	15.0	5.0	2.57	10.5	9.5	0.22
3106	3001(22) × (8)	3	6	6.8	2.2	2.95	4.7	4.3	1.13
3225	3103(1) × (5)	16	0	8.0	8.0	4.00	15.2	0.8	0.92
3361	3103(52) × (4)	7	0	3.5	3.5	2.65	6.6	0.4	0.65
3362	3103(52) × (40)	36	3	19.5	19.5	5.29	37.0	2.0	0.53

As is shown in figure 4, family 3103 might have arisen from the cross $s^{x}bu/s^{y}Bu \times s^{y}Bu/s^{z}bu$. Because of the elimination of the s^{y} male gametes, all the male gametes would be *bu* except for the few crossovers, and the expected ratio of *Bu* to *bu* in 3103 would be approximately 1:1, as was the observed ratio. If buff were linked with the *Ga* type of gametophyte genes, and the cross were *Ga Bu/ga bu* × *Ga bu/ga Bu* as shown in figure 4, the expected ratio of family 3103 would still approximate 1:1. This family, therefore, agrees with both theories. When families 3361 and 3362 are considered, it is observed that both resulted from a cross between a buff female and a non-buff male of family 3103. On the basis of linkage with the self-

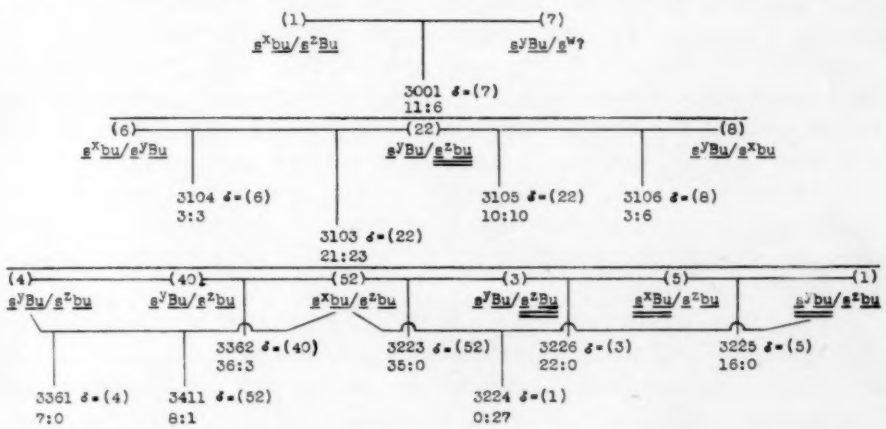

FIG. 4. A pedigree diagram of the families which show linkage between buff and the self-sterility alleles. The ratios beneath the pedigree numbers of the families are the ratios of non-buff to buff. The male parent of each family is indicated, as this is an important consideration when dealing with self-sterility as determined by oppositional genes. Crossover gametes are indicated by a double line beneath the *s* and *bu* genes of that gamete.

sterility alleles, the buff plant should be $s^{x}bu/s^{z}bu$ and the non-buff plants $s^{y}Bu/s^{z}bu$. Previous tests (Riley 1935) showed that the self-sterility class of the buff plant was $s^{x}s^{z}$. The two male plants were not listed in that paper, but they were $s^{y}s^{z}$. If these non-buff plants are crossed on to the buff female, the s^{z} gametes are eliminated in each male as are all the *bu* gametes except those that arose by crossing over. The offspring of these two crosses should contain almost entirely non-buff plants. Families 3361 and 3362 conform to that requirement. However, on the other theory, family 3103 should consist of buff plants of the genotypes *Ga bu/ga bu* and non-buff plants of the constitution *Ga Bu/Ga bu*. If such a non-buff is crossed as a male on to the buff female, approximately half the offspring should be buff, since all the pollen would function. The only way for families 3361 and 3362 to contain

almost entirely non-buff plants but also a small percentage of buffs would be for the male parent of each family to have arisen by a crossover in the male parent of family 3103, so that the constitution of 3103(4) and 3103(40) would be *Ga Bu/ga bu*. The *ga bu* chromosome would be from the female parent, while the *Ga Bu* chromosome would be a crossover chromosome from the male parent. While this is entirely possible, it is unlikely that the only two male parents selected would have both been crossover plants, since the percentage of crossing over is so low. Family 3325 also arose from a cross between a buff female and a non-buff male and contained all non-buff plants. Because of the self-sterility classes of the parents, the parental plants must each have been a crossover plant on the theory of linkage with the self-sterility alleles. On the other theory, the ratio in family 3225 could be obtained only if the male was a crossover identical with 3103(4) and 3103(40). As figure 4 shows, on the theory of linkage with *s* genes, three of the six plants selected for further study must have arisen from one crossover gamete. One would have been a crossover in the male parent of family 3103 and the other two in the female parent. On the other theory, however, four of the six plants would have arisen from crossover gametes, but in all four cases the crossing over would have occurred in the male parent. This is a less likely supposition.

If disturbed ratios are thought to be due to linkage with self-sterility alleles, the real test is the correlation between the morphological character and the self-sterility class. Unfortunately, the evidence for *Nemesia* is not too abundant, but it is consistent. If family 3103 arose from the cross, $s^x bu/s^y Bu \times s^y Bu/s^z bu$, the offspring should segregate into .049 $s^x s^z$ non-buff : .451 $s^x s^z$ buff : .476 $s^y s^z$ non-buff : .024 $s^y s^z$ buff. On the other hand, if the genotypes of the parents were $s^x s^y$ *Ga Bu/ga bu* and $s^y s^z$ *Ga bu/ga Bu*, the offspring should segregate into a ratio of .262 $s^x s^z$ non-buff : .238 $s^x s^z$ buff : .262 $s^y s^z$ non-buff : .238 $s^y s^z$ buff, because the self-sterility classes would be independent of the buff character. Unfortunately, only ten plants were tested for self-sterility classes in this family, and they segregated into an observed ratio of 1 : 2 : 5 : 2. While the numbers were too few to have much statistical meaning, there is a fair agreement between expected and observed buff types and self-sterility classes except that there are too many buffs in the last category. Better results are found in families 3105 and 3106, where a larger number of plants were tested for self-sterility alleles (table 4). Most of these plants were tested in only one direction and by only one pollinator, but both families were expected to split into only two classes, and much more elaborate tests for self-sterility groups in other families showed that if there are only two classes in a family, results are sufficiently accurate even though the plants are tested in only one direction and by only one class. These families add rather important evidence to the hypothesis that the buff gene is linked with the self-sterility alleles with about 5 per cent crossing over.

TABLE 4. *Observed ratios of non-buff to buff with the self-sterility classes of the respective families, and corresponding expected ratios assuming (1) linkage between bu and the s genes with five per cent crossing over and (2) no such linkage but assuming that bu is linked with the Ga genes. For explanation see text.*

Family		s^1s^vBu	s^1s^vbu	s^1s^2Bu	s^1s^2bu	s^vs^2Bu	s^vs^2bu	χ^2	P (df = 3)
3105	Obs.	.....	.....	2	9	8	1	.....	.....
	Exp. (1)	.....	.....	1.0	9.0	9.6	0.4	2.17	50–70%
	Exp. (2)	.....	.....	5.2	4.8	5.2	4.8	10.17	1–2%
3106	Obs.	3	1	0	5	.....	.....	.....	.....
	Exp. (1)	4.3	0.2	0.4	4.1	.....	.....	4.19	30–50%
	Exp. (2)	2.4	2.1	2.4	2.1	.....	.....	7.13	10–20%

Since both buff and pale-upper are recessive genes, some plants may be expected which would be *bubu pp*. Since no such double recessives have been identified in ten families segregating for both buff and pale-upper, even though 110 buff and 82 pale-upper plants have been found, it is highly probable that they cannot be distinguished with certainty from one of the other types and that either *bu* is epistatic to *p* or *p* is epistatic to *bu*. It is easier to test this relationship in families that do not have a self-sterility allele common to both parents, for the segregation of *bu* is greatly influenced by the gametic elimination of the gene which is coupled with the common self-sterility allele in the male. In three of the families in which there is no gametic elimination, the cross was *Bubu Pp* × *Bubu pp*. In such a cross, the theoretical ratio is 3 orange (*Bu P*) : 3 pale-upper (*Bu p*) : 2 buff (*bu P* and *bu p*) if *bu* is epistatic, and 3 orange (*Bu P*) : 4 pale-upper (*Bu p* and *bu p*) : 1 buff (*bu P*) if pale-upper is epistatic. The three families that represent this cross segregated into ratios of 4 : 7 : 6, 17 : 20 : 18, and 38 : 23 : 27. In each case, the observed ratio was closer to the expected ratio if buff is epistatic than it is to that expected if pale-upper is epistatic (table 5). One

TABLE 5. *Observed ratios of orange : pale upper : buff, and expected ratios (a) if buff is epistatic and (b) if pale upper is epistatic.*

	(a) If *buff* is epistatic				(b) If *pale upper* is epistatic			
Cross = *Bubu Pp* × *Bubu pp*								
	Orange	*pale upper*	*buff*		*Orange*	*pale upper*	*buff*	
3001 Obs.	4	7	6	$\chi^2 = 1.71$	4	7	6	$\chi^2 = 8.39$
Exp.	6.4	6.4	4.2	P = 30–50%	6.4	8.5	2.1	P = 1–2%
3002 Obs.	17	20	18	$\chi^2 = 1.66$	17	20	18	$\chi^2 = 10.34$
Exp.	20.64	20.64	13.76	P = 30–50%	20.64	27.52	6.88	P = less than 1%
3003 Obs.	38	23	27	$\chi^2 = 4.93$	38	23	27	$\chi^2 = 44.05$
Exp.	33	33	22	P = 5–10%	33	44	11	P = less than 1%
Cross = *Bubu Pp* × *bubu Pp*								
3006 Obs.	7	2	13	$\chi^2 = 0.75$	7	2	13	$\chi^2 = 5.15$
Exp.	8.25	2.75	11	P = 50–70%	8.25	5.5	8.25	P = 5–10%

family arose from the cross *Bubu Pp* × *bubu Pp*. The observed ratio was 7 orange : 2 pale upper : 13 buff; this is much closer to the ratio expected if buff is epistatic (3 : 1 : 4) than to that expected if pale-upper is epistatic (3 : 2 : 3). It seems probable, therefore, that buff is epistatic to pale-upper and that *bu* and *p* are not linked.

The relationship of orange, buff, and pale-upper is such as is occasionally caused by multiple alleles. This possibility was therefore tested. If there are three alleles such that orange is dominant over buff which is in turn dominant over pale-upper, and if an orange-colored (non-buff, non-pale upper) plant heterozygous for buff is crossed with a pale-upper, all the offspring should be orange or buff, and no plants should be pale-upper. In four families from a cross between an orange and a pale-upper, all three types were recovered. If orange is dominant over pale-upper which is in turn dominant over buff, a cross between two orange-colored plants could not produce all three types. In one family from two orange-colored parents, all three types were recovered. Apparently a two-factor hypothesis with epistasis of buff is more satisfactory than any hypothesis based upon multiple alleles.

There is a small amount of evidence indicating that *o* and *bu* are not linked. Since *bu* is not differentiated from *Bu* in the *oo* plants, the ratio of orange to buff must be used to determine whether there is any linkage. One family segregated into 6 orange : 4 buff : 15 white and another segregated into 9 orange : 13 buff : 19 white. In each case the parents were *Oo Bubu* × *oo bubu*, and in neither case was the deviation from a 1 : 1 ratio significant to suggest linkage. It must be remembered, however, that the populations in these families were small.

When orange-colored flowers were placed in hydrochloric acid vapor, the orange color became much paler. It is possible that the paler color in types such as buff and pale-upper may be due to a higher acidity in the cell sap of some of the epidermal cells of the limb in such plants.

Glass-green (*gl*). In the glass-green type, the corolla limb varies from Sea-foam Yellow to Pale Glass Green and frequently is so pale as to be almost indistinguishable from white. The tube is orange with or without dark purple spots.

Glass-green behaves as a simple recessive to white. In six instances, two white plants were crossed which must have been heterozygous for glass-green. In one family, the parents were also heterozygous for yellow and for yellow-spot, which complicates the picture, but in the other cases both white and glass-green appeared in the progeny and in four of those families the ratio was approximately 3 : 1. In the fifth family the ratio was 26 : 2, but even in this case the deviation divided by the standard error does not greatly exceed 2 and this family can probably be considered as segregating into a 3 : 1

ratio. In four of the families one self-sterility allele was common to both parents. The close approximation to a 3:1 ratio in these families indicates that glass-green is not linked with the self-sterility alleles. In two families which resulted from reciprocal crosses between two glass-green plants, all the offspring were glass-green. Four families from a cross between a white-flowered plant which must have been homozygous for the allele of glass-green and a glass-green plant contained 132 plants and all were white. It is probable that glass-green is a simple recessive; the gene for this type will be identified by the symbol *gl*.

The relationship between orange and glass-green is indicated by two families. One family arose from a cross between an orange and a white both of which were heterozygous for the anthocyanin gene. The non-anthocyanin offspring segregated into 6 orange non-buff : 4 orange buff : 13 white non-glass-green : 2 white glass-green. It was not possible to distinguish orange glass-green or buff glass-green types from the orange non-glass-green and buff non-glass-green plants, which would indicate that *O* is epistatic to *Gl* and *gl*. That *gl* and *bu* are not one and the same gene which merely exerts a different reaction depending upon whether it is combined with *O* or with *oo* is shown by the fact that the non-buff and buff types are segregating 1:1 while the white and glass-green types are in a ratio of 3:1. Other evidence to support this is the fact that buff is linked with the self-sterility alleles while glass-green is not. The second family came from a cross between orange and white (plus anthocyanin). The non-anthocyanin plants segregated into 9 orange non-buff : 13 orange buff : 10 white non-glass-green : 9 white glass-green. In this family, also, *O* appeared to be epistatic to the *Gl* and *gl* genes, just as *o* appeared epistatic to *Bu* and *bu*. In this family the orange non-buff plants further segregated into a ratio of 7 non-pale-upper : 2 pale-upper. The fact that the white plants of the same family were segregating into 1 non-glass-green : 1 glass-green indicates that pale-upper and glass-green are not the result of one and the same gene acting upon a different background. There is insufficient evidence to show whether *o* and *gl* are linked.

Yellow (*y*).[4] There appears to be a type which in many ways resembles buff phenotypically but which appears to be due to a recessive gene acting together with the homozygous *o* gene. Unfortunately, the evidence for the inheritance of this yellow type is not so extensive as might be desired, since yellow in the original material was confused with buff. After tracing buff through several generations, it was realized that it is a modification of orange and is never expressed in an *oo* plant and that the yellow plants were found only in a line that was homozygous for *o*. When it was realized that these two

[4] This symbol should not be confused with the *Y* of a preliminary paper (Riley 1940) which has now been replaced by *O*.

types were genotypically different, it was too late to carry out any further tests, for seeds from the yellow strains were no longer viable.

One family of this original material segregated into 25 non-yellow to six yellow, which would indicate that yellow was recessive. Of the non-yellows, 20 were white and five were glass-green. The segregation into 20 white : 5 glass-green : 6 yellow indicates, although the data are not too numerous, that yellow may be epistatic to glass-green. On this assumption, chi-square for this family equals 0.89. Two families arose as reciprocal crosses between a heterozygote and a yellow and yielded respectively 54 white : 35 yellow and 7 white : 9 yellow. One other family segregated for yellow but will be discussed under the section dealing with the gene for yellow-spot. Apparently yellow is a simple recessive. The symbol for the yellow gene will be *y*.

Linkage between *y* and *o* and between *y* and *gl* has not been tested.

In 1940, a type listed as yellow was purchased and crossed with white. These yellow plants varied in depth of color from Lemon Yellow to almost Glass Green. Whether they represent the old *y* gene cannot be stated at present. Seeds from crosses of these yellow plants were not sown for three years and the only seeds to germinate were from a cross between a pale yellow and a blue. The F_1 plants were white. The non-blue F_2 plants were difficult to classify because the yellows were pale, but the yellow type appeared to be less frequent than the non-yellows. Further tests with this type are being made.

Yellow-spot (*ys*). The yellow-spot type is not so well defined in its expression as are some of the other types. The yellow color appears as a large number of dots or streaks radiating out on the lower lip from a small area near the throat (fig. 3). The remainder of the lower lip may be white or Seafoam. The upper lip appears to be entirely white or Seafoam.

In *oo* plants, yellow-spot appears to be recessive to non-yellow-spot, although two families are puzzling. The gene for yellow-spot will be designated *ys*. Ten families resulted from crosses between two heterozygotes, but only seven yielded ratios in which the deviation from a 3 : 1 ratio divided by the standard error was less than two. In one family the ratio was 27 *Ys* : 1 *ys*, resulting in a deviation only 2.62 times the standard error, but in the other two families the ratios were very puzzling, for it appeared as if yellow-spot were dominant. The ratios were 4 *Ys* : 14 *ys* in one family and 2 *Ys* : 7 *ys* in the other. It was thought that perhaps linkage with *s* genes was the explanation, but this does not seem to be the case. In the second family no self-sterility allele was common to the two parents, while in the first there was a common self-sterility allele, but even with such linkage the observed ratio would not be probable and the reciprocal cross gave a fairly good 3 : 1 ratio (16 *Ys* : 3 *ys*). It may be that these two ratios are disturbed because of the difficulty of distinguishing between yellow-spot and non-yellow-spot in

families that have certain combinations of other genes, but there is no evidence that this is so.

One family arose from a cross between two white-flowered plants which were heterozygous for the gene for blue-margin (Riley 1940). This family segregated into 38 white : 54 of a yellow color. The parents of this family are both to be found in a family which is segregating for yellow and for glass-green, and therefore may presumably be heterozygous for *y* and for *gl*. Four sibs of the two parents are heterozygous for the gene for yellow-spot, so presumably the parents of this family might both be *Glgl Yy Ysys*. In that case, the offspring should segregate into a ratio of 27 white to 37 of all the three yellow types. On a white non-blue-margin background, yellow is possibly epistatic to glass-green, but yellow, yellow glass-green, yellow yellow-spot, and yellow glass-green yellow-spot cannot be distinguished from one another, and glass-green and glass-green yellow-spot can be distinguished only with difficulty. In blue-margin plants it is almost impossible to differentiate phenotypically any of these three types with yellow color. In studying this family, then, all the yellowish plants were classed together. On the basis of a three-gene difference and treating the case as one of complementary genes, the expected ratio becomes 39 white : 53 yellowish. The observed ratio fits this hypothesis remarkably well, for the deviation divided by the standard error is only 0.17.

Linkage of *ys* with *o*, *gl*, and *y* has not been tested. Because *bu* and *p* cannot be differentiated on a *oo* background, and because *gl*, *y*, and *ys* cannot be differentiated on a *O* background, any linkage between either *bu* and *p* with *gl*, or *y*, or *p* cannot be determined directly.

Sectorial Chimaeras. Lawrence (1931) has pointed out that sectorial chimaeras may sometimes be used to detect recessive genes. These chimaeras may be the result of mitotic abnormalities resulting in somatic nondisjunction. If this occurs in a young bud of a heterozygote, and the chromosome bearing the dominant gene becomes lost, the tissue that develops from it will have only the recessive gene. If this tissue is one that the gene affects directly, it will be phenotypically recessive. Such situations are infrequent in *Nemesia*, but have been encountered occasionally when thousands of flowers were examined.

In one plant of one family from the cross $OO \times Oo$ and in one of a family that arose from the cross $OO \times oo$, a white chimaera was found on an orange-colored flower. Half the plants of the first family and all of the second are *Oo*. The chimaeras therefore were probably the result of the loss of the *O* gene in heterozygotes and confirm the breeding data that orange is dominant over white. One flower of plant 3209(1) had a yellow chimaera on the upper lip of an otherwise white-flowered plant. The parents of 3209 were 3111(4), which is homozygous for *Y*, and 3112(11). Family 3112 was

segregating into 3 white : 1 yellow, so plant 3112(11) might well have been *Yy*. If so, half the plants of 3209 would be *Yy* and presumably plant 3209(1) was one of these plants. This is a further indication that yellow is recessive to white and is different from orange.

SUMMARY

Six genes for yellow or orange flowers have been found in *Nemesia strumosa*. The white-flowered type is regarded as the standard.

Gene *O* produces a deep yellow or orange color on both the upper and lower lips of the corolla. The color of *O* plants is usually Cadmium Yellow or Light Cadmium but in a few cases is Orange. Plants with the *O* gene may have the color diluted by two other genes, *bu* and *p*. Gene *p*, pale-upper, lightens the color of the upper lips to approximately Apricot Yellow, while *bu*, buff, changes the upper lips to Sulfur Yellow and the lower lips to Buff Yellow. Both genes show a slight variation from these hues depending probably upon modifying genes. Gene *o* is epistatic to *p* and *bu* which are therefore expressed only in the presence of *O*. Gene *bu* is epistatic to *p*, so that *O- pp bubu* and *O- P- bubu* plants are indistinguishable. Gene *bu* is linked with the self-sterility alleles. All *O- P- Bu-* plants are orange.

Three genes produce some yellow color in *oo* plants but apparently are not expressed in the presence of *O*. Gene *y*, yellow, produces yellow-colored flowers. This is recessive to *Y*, non-yellow, although the behavior appears to be somewhat erratic and the ratios disturbed. The gene for glass-green, *gl*, produces flowers in which the corolla limb is Glass Green or Seafoam Yellow. It is recessive to *Gl*, non-glass green. The yellow-spot gene, *ys*, produces a yellow spot with yellow lines radiating from it on the lower lip of the corolla near the throat. Yellow appears to be epistatic to glass-green and possibly to yellow-spot. Glass-green non-yellow-spot and glass-green yellow-spot plants have not been distinguished and it is not known which is epistatic. Plants with the constitution *oo Y- Gl- Ys-* are white.

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THE VARIATIONS AND ORIGIN OF BOTRYCHIUM LANUGINOSUM[1]

M. A. CHRYSLER

Botrychium lanuginosum Wall. ex Hook. & Grev., a remarkable Asiatic species, is closely related to *B. virginianum* (L.) Sw., but differs in having the fertile spike or segment inserted in a position subject to variation, generally above the level of the two basal pinnae. On the basis of 24 specimens from several American herbaria, a brief article (Chrysler 1925) called attention to the significance of this species from a morphological standpoint. In 1938, a visit to London afforded an opportunity to study the large collections at the British Museum and at Kew. During recent months additional specimens have been made available by the following herbaria:

Amherst College
Botanical Garden, Buitenzorg, Java
University of California at Berkeley
Chicago Natural History Museum
Cornell University
Royal Botanic Garden, Edinburgh
Gray Herbarium, Harvard University
University of Michigan
Missouri Botanical Garden
New York Botanical Garden
Philadelphia Academy of Natural Sciences
Princeton University
United States National Museum
Yale University

It is a pleasure to acknowledge my indebtedness to the curators of these herbaria. All told 217 specimens have been examined, representing all parts of the range of the species, which may be roughly traced thus: N. W. India, Ceylon, New Guinea, Philippines, Tibet. A few of the specimens take the form of photographs, especially that of the type sheet, which Ballard (1940) has located at Edinburgh and with great kindness has photographed for my use. Thanks are due also to Dr. H. H. Bartlett for furnishing information on certain points from his field experience, and for the loan of sheets from his valuable series, No. 6560, illustrating variation. Dr. R. T. Clausen has been good enough to read the manuscript.

NOMENCLATURE

Botrychium lanuginosum first appears as Number 48 in Wallich's *List* (1828), as a *nomen nudum*. Besides the type sheet in Greville's herbarium at the Edinburgh Botanic Garden, consisting of two plants and annotated "48. Napalia. E.I.C," there is at the British Museum a sheet bearing five plants and labelled "Nepal, 1821, Dr. Wallich No. 48"; at Kew a sheet

[1] Publication of Bureau of Biological Research, Rutgers University.

inscribed "Kamoun Wallich 1829 Type number"; a second: "Nepalae 1821 Type number"; a third (in Hooker's collection): "*Osmunda lanuginosa* Wall. Napalia 1821" bearing two specimens; at the U. S. National Museum a sheet consisting of one complete plant and bearing a British Museum label inscribed: "*Botrychium lanuginosum* Wall. = *B. virginianum* Sw. Nepal 1821. Wallich 48." How many of these plants were collected by Wallich is open to question. In 1829 Hooker and Greville presented a formal description of the species as explanation of their plate 79, the origin of which from the Edinburgh sheet has been forcibly argued by Ballard (1940). This sheet may hence be considered the type. But it is unfortunately true that over 90 per cent of the plants labelled *B. lanuginosum* which I have examined conform neither to plate 79 nor to the description, although the larger plant of the Edinburgh sheet is an excellent example of what has ordinarily been called *B. lanuginosum*, having the fertile spike inserted above the two basal pinnae, and lacking only the basal part of the *bulbus* bearing lanugo at its apex. Ballard has offered the plausible explanation of the drawing of plate 79 as a combination of the two plants of the Edinburgh sheet. Dr. R. T. Clausen's remark upon seeing the photograph of this sheet was that probably Hooker and Greville considered that the larger plant was abnormal. From the material available to these authors they seem to have had their minds fixed on a plant having the habit of *B. virginianum* (*frondem infra apicem gerens*) but possessing *bulbus ovatus, subsquamosus, apice lanigerus*, and this is exactly what is represented in plate 79. Beddome's (1863) drawing more nearly conforms to current conceptions of the species, representing a leaf in which the fertile spike occupies a position above the fourth pinna. In 1833 Hooker acknowledged that he had had access only to very small specimens, and amended his earlier description thus: "In general the insertion of the scape is above the lower primary division of the frond." Presl adopted the corrected description in his *Supplementum* (1845). Doubts arose as to the distinctness of *B. lanuginosum*, as appears in Moore's *Index* (1857) where it is listed as a variety of *B. virginicum* Willd.: "β *lanuginosum* M." To this point of view Milde (1864) objected on the following grounds: (1) the higher level of insertion of the fertile spike, (2) straight form of the epidermal cells *vs.* the flexuose form in *B. virginianum*, (3) catadromy of the secondary branches of the frond *vs.* the anadromy of *B. virginianum*. Milde's monograph (1869) emphasizes the last feature and regards the plant which was represented by Hooker and Greville as a juvenile specimen. Clarke (1880), who had the benefit of field experience, was not impressed by the catadromy as a safe distinction, and considered all of the Himalayan material to be one species. Hope (1903) presents additional observations on this and related questions. He regards *B. lanuginosum* as a distinct species, as do other students of the group, such as Bitter (1900), Christensen (1906), and Clausen (1938).

ANALYSIS OF THE SPECIMENS

As the foregoing paragraph implies, *B. lanuginosum* is closely related to *B. virginianum*. Hooker and Greville's treatment would clearly indicate such relationship. The specific name would suggest a practical distinction, but it may readily be verified by inspection of a fair-sized series of the latter species that lanugo may be present at the base of the stipe, also to a lesser extent at regions of branching of the leaf. Moreover some specimens of *B. lanuginosum* are almost entirely glabrous, a condition which cannot be attributed altogether to wear. Nakai (1925) has in fact distinguished the variety *leptostachyum*. Lanugo is much more apt to characterize large specimens, where it sometimes clothes the entire stipe. Otherwise Hooker and Greville's characterization, *Bulbus ovatus, sub-squamosus, apice lanigerus*, agrees with later observations. The *bulbus* moreover seems to be an important character; the base of the stipe in *B. virginianum* would not impress one as bulbous, while in *B. lanuginosum* it is definitely swollen. Concerning the anadromous *vs.* catadromous distinction it may be well to recall a remark of Clarke (1880): "the lowest primary pinnae are often twisted in drying." It is easy to demonstrate anadromy in *B. virginianum*, but such observations as I have been able to make on herbarium material of *B. lanuginosum* confirm Clarke's statement that while there is a strong tendency to be catadromous, the secondary pinnae are often nearly opposite and sometimes they are slightly anadromous. The character hence appears to have little value as a practical distinction.

The variations shown by the leaf may be grouped in four "plans," as follows:

(1) The *virginianum* plan, in which the fertile spike is attached (adaxially) at the base of the frond (fig. 1). As clear examples may be cited: University of California No. 588663, collected by R. R. Stewart in Mussoorie (N. W. India); University of Michigan, collected by H. H. Bartlett as No. 7912 in Habinsaran, Sumatra. Both of these show the bulbous enlargement at the base, with a moderate amount of lanugo.

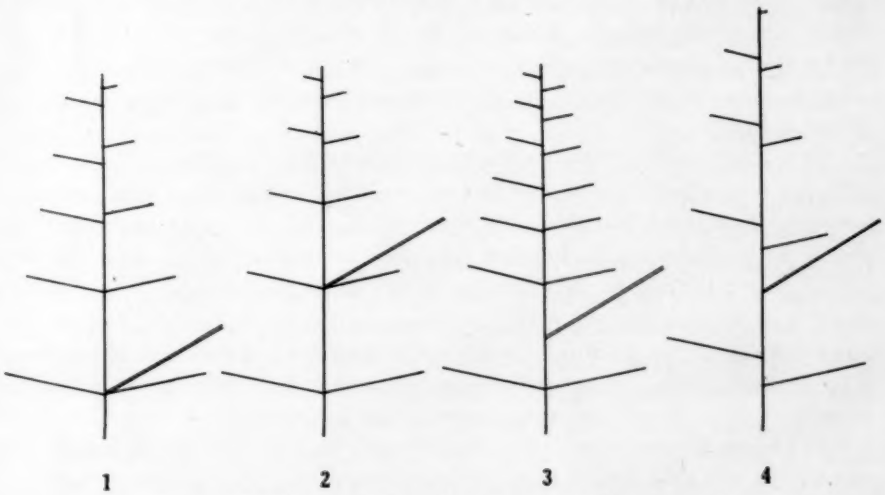
(2) The fertile spike arises in median position accompanying two sterile pinnae which belong to the second node of a leaf rather than to the basal node (fig. 2). This plan may be visualized as a plant of *B. virginianum* having an extra pair of sterile pinnae below the normal "trio" of two sterile pinnae and the fertile spike.

(3) The pinnae are opposite in arrangement except near the apex of the leaf; the fertile spike arises between the nodes formed by the bases of opposite pinnae, generally between the first and second nodes (fig. 3). In a large number of plants it may be distinctly seen that the fertile spike arises adaxially.

(4) The pinnae are strictly alternate throughout the leaf, except that

the alternation is interrupted by the fertile spike, which in about 75 per cent of the plants assigned to this plan is inserted between the second and the third pinna, and may frequently be determined as adaxial even though in pressing it has been bent over to one side (fig. 4).

Over thirty plants lying between plans 3 and 4 present interesting conditions. For instance, a specimen collected in Assam by G. Mann (in the Buitenzorg Herbarium) shows a basal pair of pinnae, followed by the fertile spike which is considered to represent the fusion of two (Chrysler 1910), next by two pinnae arising only 3 mm. apart. Then comes an 18 mm. space followed by two pinnae 3 mm. apart, and so on. Evidently the tendency to



FIGS. 1–4. Diagrams of plans 1–4; for explanation see text.

the opposite plan is present, but fully expressed only in the basal pinnae and the fertile spike. If the prevailing conception of a fern leaf as essentially a scorpioid sympodium is adopted, this leaf exemplifies the exceedingly frequent type in which the apex retains the primitive condition while, as the base is approached, the pinnae become nearly or quite opposite. This condition is common in *B. virginianum* (see also figure 1). Plants of this type occasionally show a zigzag plan, strongly suggestive of a sympodium.

Occasional specimens have been met in which a fertile spike appears to be paired with a sterile pinna. To illustrate this condition sheet No. 1429168, U. S. National Museum, may be cited. Certain other plants are better interpreted as belonging to plan 1. There is no inherent reason why two opposite pinnae, each with a single vascular bundle but one pinna fertile, should not occur as an abnormality, especially in view of the observation of sterile pinnae bearing a few sporangia. Bitter (1900) refers to these plants as "not

rare''; very few such plants have been found in the present study. Hope (1903) describes a plant having a small fertile pinnule on one of the lower pinnae. Another abnormality mentioned by Bitter is the presence of a second, smaller, fertile spike borne on the costa further toward the apex; this condition is very rare in the plants which have come to my attention, and may be exemplified by the British Museum sheet labelled ''Ceylon, Gardner 1781. 1846.'' One of the three plants on this sheet shows an extra fertile spike arising close to pinnae 8 and 9.

In view of the frequency of plants of *B. dissectum* var. *obliquum* (Muhl.) Clute showing forking or paired fertile spikes (Chrysler 1910, 1925), it should be recorded that a single large specimen of *B. lanuginosum* from Pulney Mountains, India, S. B. Fairbanks donor, deposited in the herbarium of Amherst College, shows a spike which 50 mm. from its base divides into two not quite equal branches, each continuing a distance of 80–90 mm.

In my paper of 1925 reference was made to plants with the fertile spike alternating with sterile pinnae and presumably occupying a similar lateral position. This condition was illustrated as figure 1 of the article cited. The figure in question shows the leaf-branches arranged thus: pinna No. 1 L (left); No. 2 R (right); No. 3 is the fertile spike (apparently R); No. 4 L; No. 5 R, continuing in alternate succession to the apex. It should be emphasized that, with the uniform exception of the fertile spike, departures from a strict R, L, R, L, . . . succession are extremely rare in representatives of plan 4. If then the fertile spike of the plant in question represents a single fertile pinna, it should belong to the left side, and number 4 instead of arising on the left side should come from the right side of the axis. If however the fertile spike is interpreted as a fused pair of pinnae, the normal alternation is at once restored. The two interpretations may be represented thus:

(Apparent): No. 1 L; No. 2 R; No. 3 R (fertile); No. 4 L; No. 5 R; . . .
(Theoretical): No. 1 L; No. 2 R; No. 3+4 (L+R) fertile; No. 5 L; No. 6 R; . . .

The second interpretation brings this specimen into line with plan 4 of an earlier paragraph. Two points of evidence are however lacking: first, the number of vascular bundles in the stalk of the fertile spike; second, signs of twisting which would indicate that the fertile spike is truly adaxial in position. But so many plants in plan 4 have been seen in which the fertile spike is obviously adaxial that a lateral position should be accepted only on sufficient evidence and moreover regarded as extremely exceptional.

The care with which each plant must be examined can not be better shown than in the case of U. S. sheet No. 456830, consisting of a plant collected in Yunnan, China by B. Henry, No. 9213B. At first sight this plant seems to illustrate the alternate arrangement, shifting to opposite beyond the middle of the blade, thus:

No. 1 L; No. 2 fertile; No. 3 L; No. 4 and 5 nearly opp.; No. 6 and 7 nearly opp.; becoming alternate toward the apex. But a lens discloses a slight scar almost opposite No. 1; also nearly opposite No. 3 is a mark where another pinna has apparently been cut off with a sharp instrument. Moreover the fertile spike arises from behind the leaf as it is mounted. The plan should hence be changed to read:

No. 1 L (and 2 R); No. 3 + 4 fertile; No. 5 L (and 6 R); No. 7 and 7, . . . The plant is plainly an example of plan 3.

The four plans which have been distinguished may now be more critically examined. Plan 1 occurs in a very small number of the specimens (about five per cent), and the question at once arises whether they should be assigned to *B. lanuginosum*. They agree well with Hooker and Greville's description and their illustration, but not at all with subsequent treatments of the species. In some of the twelve plants included in this plan the fertile spike and two sterile pinnae do not arise at quite the same level, but the three form a group or trio. The exact insertion is hard to determine because the fertile spike is apt to be markedly decurrent. Not only is this condition evident externally but the vascular strands of the spike descend very gradually through the cortex of the axis before becoming attached to the C-shaped group of petiolar bundles, in contrast to the strands belonging to the sterile pinnae. These strands can sometimes be seen in a pressed specimen, although in critical cases only a series of transverse sections would determine the exact level of attachment of the two sets of bundles. Serial sections through *B. virginianum* show that the spike is attached below the basal pinnae; no material of plan 1 has been available for sectioning. Eight of the plants are small and may be regarded either as depauperate or as young plants. The labels state that two of the plants grew "on rocks," a third "on earth about limestone ledges." But several are medium or large specimens. Of special interest is one of the three plants collected by E. B. Copeland as No. 1848 on Luzon, P. I., and shown in its natural size in figure 5. Two pinnae and the fertile spike arise quite close together, followed by an interval of about 6 mm. distal to which is an almost equal dichotomy. The leaf apparently belongs to a young plant and might be interpreted as a sympodium.

Plan 2 is closely related to plan 3 since in both cases the pinnae are arranged on the opposite plan. Since the exact region of attachment of the fertile spike is open to question as in plan 1, it may well be that certain of the plants listed in plan 2 really belong in plan 3. In fact it is probable that all of them do, on the basis of attachment of the vascular strands, but plan 2 is sufficiently distinguished externally to warrant separation of the 22 plants which have been listed in this group. Of the 68 other plants showing the opposite arrangement (plan 3), 52 have the fertile spike inserted between

the first and second nodes of the leaf, 15 between the second and third nodes, and one between the third and fourth nodes. It has been shown (Chrysler 1925), in the one plant of this group from which serial sections have been prepared, that the vascular supply of the fertile spike arises as two strands, one from each side of the C-shaped bundle system of the rachis; these strands gradually approach the adaxial region and extend upward through the spike. These observations parallel the ones earlier made on *B. virginianum*, and indicate that the spike is a double organ, the equivalent of a pair of leaf-branches, and explain how it comes to have the adaxial position.

FIG. 5. E. B. Copeland's No. 1848; for explanation see text.

Eighty-four plants have been listed as belonging to plan 4; of these 65 resemble the type plant plotted in figure 4, having the fertile spike between pinnae numbers 2 and 3, in the adaxial position and representing a pair of leaf-branches. In five plants the spike arises between pinnae 1 and 2, in eight between pinnae 3 and 4, in five between pinnae 4 and 5, and in one between pinnae 6 and 7. Reference to figure 4 readily shows that the leaf is arranged on the alternate plan only when the fertile spike is counted as two fused pinnae. The figure also brings out the unequal internodes, short ones alternating with longer ones. The prevalence of this condition indicates that the leaf in this species is well on the way to the opposite arrangement of pinnae. It will be noticed that in plan 4 as well as plan 3 the great majority (76–77 per cent) of the plants have the fertile spike situated above the second pinna.

The readiness with which most specimens may be classed as of the alternate or the opposite plan suggests that two varieties or species may be represented. In order to test whether such supposition has any geographical basis, the distribution of 160 plants for which the place of collection is definitely stated on the label has been plotted on an outline map. Almost all of the collections have been made either in the Himalayan region of India and adjacent China, or in a southern belt including the Nilgiri Hill region of India, Ceylon, and East Indies (an isolated group of stations in Luzon, P. I., has been omitted). The tally stands thus:

Northern belt—49 alternate, 40 opposite

Southern belt—19 alternate, 52 opposite

There is hence no clear geographic segregation. The best that can be said for the case is that in the southern part of the range there appears to be a tendency for the opposite arrangement to prevail. Moreover, eleven plants, included in H. H. Bartlett's number 6560, collected on Deleng Piso-piso, Sumatra, present examples of both opposite and alternate forms. As an extreme case may be cited a sheet at Kew: "Herb. J. S. Gamble, Mysore District no. 3087," bearing two leaves growing from the same base, one being opposite in plan and the other alternate! Further, the plants intermediate between plans 3 and 4 offer difficulties. If however the alternate plan is regarded as standing closer to the ancestral leaf-pattern, the predominance of alternate individuals in the Himalayan region compared with the southern belt agrees well with the opinion of Butters (1917): "*Botrychium virginianum* and its allies have a typical boreal distribution and all the tropical forms of this group have evidently come from the north." In this connection it may be well to recall that there is in South Africa a single species, *B. chamaeconium* Bitt. et Hieron. With great kindness Mr. Ballard has furnished me with a photograph of the type specimen; this clearly shows a plant of the opposite plan.

PHYLOGENY

The position of the fertile spike in *Botrychium* looks like a case of "phylogenetic slide." But the direction of sliding is not yet certain. There are three possibilities:

1. *B. lanuginosum* is a primitive, still plastic species. Earlier in this study the apparently lateral origin of the fertile spike and its variable position along the leaf-axis suggested that this species had not settled down to the condition which occurs in *B. virginianum et al.* Familiarity with a much larger amount of material leads to the conclusion that laterally inserted spikes are extremely rare, while adaxially inserted spikes, some with visibly double vascular supply, are plentifully represented, even in plants where the sterile pinnae are alternately arranged. Examples of a fertile

spike paired with a sterile pinna also are exceedingly rare if not indeed capable of a different interpretation. In this inquiry the anatomist is hampered by inability to study serial sections of critical specimens. These considerations suggest that the fusion of two leaf-branches to form a fertile spike originated at a date prior to the "wandering" of the spike from one level to another. Hence the second possibility.

2. *B. lanuginosum* represents a youthful species, still in the plastic condition, which has arisen from the *virginianum* type (not necessarily from *B. virginianum*), perhaps in connection with migration from north temperate regions to the moist tropics. It should be noted that the largest plants of any species of *Botrychium* are found in *B. lanuginosum*, some spreading over two herbarium sheets, e.g., a specimen at Yale University, collected in Ceylon by G. Wall (see also Bitter 1900, Hope 1903). By "plastic" is here meant the variability in extent of the phylogenetic slide, with a tendency for the spike to settle down in the position above the first two pinnae. It may be that the decurrent feature of the spike is an indication of an upward slide, although it may also be interpreted as an accompaniment of the upright position of the spike *versus* the dorsiventral habit of the photosynthetic parts of the plant. The small specimens having the *virginianum* plan would represent juvenile plants, according to the second view. Moreover, Clausen's (1938) opinion that *Sceptridium* represents the most primitive division of the genus would suggest that the fusion of sterile and fertile parts began far down on the shoot axis and has moved progressively toward the apex. Again, the imperfect shift from the anadromous to the catadromous condition is in accord with the advanced position given to *B. lanuginosum* in this second possibility.

3. There is finally the stimulating proposal of Zimmermann (1930) and Bower (1935) that the division of the *Botrychium* leaf into fertile and sterile branches represents an ancient antero-posterior dichotomy. Without attempting at present to discuss this "possibility" it may be remarked that it obviously implies a very advanced position for *B. lanuginosum*.

SUMMARY

An attempt is here made to analyze the plans presented by the extremely variable *Botrychium lanuginosum*. On the basis of the position of attachment of the fertile spike, and the opposite *vs.* alternate arrangement of the pinnae, the specimens, numbering 217 and representing the known range of the species, are placed in four groups. The analysis suggests that there has been a phylogenetic slide of the fertile spike, probably in the distal direction. If this view is adopted, the species must be regarded as an advanced, still unstable member of the family.

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THE DISCOVERY AND DISTRIBUTION OF CINCHONA PITAYENSIS IN ECUADOR[1]

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The United States faced a dangerous shortage of quinine early in 1942, when the Dutch East Indies passed into the hands of the Japanese. In an effort to find new supplies of this essential antimalarial drug, the Board of Economic Warfare established Cinchona Missions in the several South American republics which had once been the only source of quinine. However, the exploitation of wild *Cinchona* barks had always been an uncertain and hazardous business, and could not compete at all with easily-harvested plantation barks of much better quality. Consequently, as the plantations of Java and Sumatra came to produce ninety-five per cent of the world's quinine supply, wild barks from South America practically disappeared from the market. The problem of reviving this extinct industry had to be solved by botanists, since *Cinchona* trees must be found and identified before procurement of bark could even start.

In the fall of 1942, Dr. F. Raymond Fosberg and I were sent to Colombia by the Board of Economic Warfare, to start the first *Cinchona* surveys at once. We were able to localize substantial quantities of *Cinchona officinalis* and *C. pubescens*, as well as *Remijia pedunculata* (Steere 1945a). However, in March, 1943, we were unusually fortunate in our rediscovery of *Cinchona pitayensis* in the Cordillera Central of southern Colombia, in the Department of Cauca. The type locality of this species, which was supposed to have a rather restricted geographical range, is the village of Pitayó, on the slopes of the Nevado del Huila, north of Popayán. Karsten (1858) made further collections on the slopes of the Colombian volcanos of Cumbal and Chiles, in the Department of Nariño, but no other early collections are known. Even though it was little known to botanists, *Cinchona pitayensis* was of very considerable commercial and pharmaceutical importance just about a century ago. The supply was apparently soon exhausted, however, and the species became so rare that it was nearly forgotten. At the time of our surveys it had been left to reëstablish itself for several decades, and we found that it occurred not only in a much greater quantity than we had anticipated, but also over a much wider area.

As Karsten had collected *Cinchona pitayensis* on the Colombian side of the Volcán de Chiles, which is exactly on the Colombian-Ecuadorian frontier,

[1] Paper from the Department of Botany and the Herbarium of the University of Michigan.

an extension of the geographic range of this species into Ecuador could be predicted with some certainty, although it had apparently never been collected there, and is not mentioned in any of the classic works on Ecuadorian botany which treat the Rubiaceae (Jameson 1865; Standley 1931; Diels 1937).

A Cinchona Mission was finally established in Ecuador during the late spring of 1943, and I transferred my field surveys there from Colombia in July, 1943, in order to explore the northern provinces, where no *Cinchona* species were known. The northernmost province, Carchi, was the most logical point to begin the search for *Cinchona pitayensis*, and the provincial capital of Tulcán made an appropriate center of operations. The first survey was made east from Tulcán, over the Cordillera Oriental, in the valley of the Río Chingual. Although *Cinchona officinalis* was discovered for the first time in northern Ecuador, no *C. pitayensis* was found. My second exploration trip in Ecuador was made west from Tulcán, by way of the frontier village of Tufiño. The trail runs somewhat southwest from Tufiño and crosses the Cordillera Occidental on the south shoulder of the Volcán de Chiles by way of a pass at 4500 m. altitude. West of this pass, on the southwestern slopes of Chiles, I found several large stands or "manchas" of *Cinchona pitayensis* (*Steere 8043*, 22 August 1943). Residents of Carchi told me that *Cinchona* bark or "cascarilla" from such high altitudes could not possibly be of any value, as their good bark all came from Maldonado, farther down the same trail, at an altitude of 1500 m. or lower. However, they were finally convinced that this bark might have some value —it is extremely bitter in the field—and agreed to search for more manchas on other ridges in the same region.

After the original discovery of *Cinchona pitayensis* in Ecuador, many other surveys were made to determine its geographical distribution in the country. Large amounts were found almost at once all along the western slopes of the Cordillera Occidental between the Colombian frontier and the Río Mira, in the Province of Carchi. The largest quantities were found west of El Angel, and still farther west, on the slopes of the isolated Cerro Golondrinas. *Cinchona pitayensis* also exists in the Cordillera Oriental of Carchi, in the region of Huaca. With a survey party, I crossed this range south of Huaca, by way of the enormous Hacienda Indúgel, reaching the headwaters of the Río Cofanes, in the Oriente. Some trees were found on both sides of the eastern range, but no large manchas which would justify exploiting this almost inacessible region (east side, *Steere 8125*, 22 October 1943; west side, *Steere 8153*, 27 October 1943).

At first, I had the idea that *Cinchona pitayensis* would be found only in Carchi, the northernmost province of Ecuador, at least in the western Andes. This supposition was based on the phytogeographical fact that the "fraile-

jón," *Espeletia Hartwegiana*, which is a common and conspicuous element of the Colombian páramos, and forms the dominant high-páramo vegetation in Carchi, does not extend farther south in Ecuador than the Río Mira. Many other elements of the southern Colombian flora are also restricted in Ecuador to the Province of Carchi. Since *Cinchona pitayensis* occurs not far below the páramo, between altitudes of 2500 and 3200 m., I had assumed that it, likewise, would have its southward distribution limited by the deep, desert valley of the Chota and Mira rivers. Therefore, the discovery of substantial quantities of it in Imbabura Province, south of the Río Mira, had considerable botanical significance as well as economic importance. My first survey in Imbabura was made late in November, on the southwest slope of Volcán de Cotacachi, west of Otavalo, in the company of W. B. Drew and F. M. Ownbey. Along an old trail to Intag, through a region called Selva Alegre (for some unknown reason!), substantial quantities of *Cinchona pitayensis* were found (*Steere 8191*, 3 December 1943). Later in December, working alone, I explored the Colonia Buenos Aires, just south of the Río Mira, northwest of the Volcán de Cotacachi, and found that the zone between 2500 m. and 3000 m., as in other regions, contained abundant *C. pitayensis* (*Steere 8201*, 15 December 1943). Later surveys in Imbabura by other botanists of the Cinchona Mission, especially by W. B. Drew, demonstrated that the band of *C. pitayensis* extends from the Río Mira south to the Río Guayllabamba, at appropriate altitudes, thus reaching the northernmost part of the Province of Pichincha.

In May, 1944, *Cinchona pitayensis* was discovered on the western slopes of the Volcán de Pichincha, very near Quito. This important discovery resulted from a field observation of plant associations, and demonstrates clearly the value of our study of associated plants, especially members of the Rubiaceae (Steere 1945b). In the zone of the Río Plata, in northernmost Carchi Province, where *Cinchona pitayensis* was first found, an associated plant was *Cephaëlis Jamesonii* Standl., another member of the Rubiaceae (*Steere 8039*, 22 August 1943; *Steere 8093*, 6 October 1943). This fact in itself had no significance until many different stands of the *Cinchona* had been discovered in the provinces of Carchi and Imbabura, and it was noted each time that the *Cephaëlis* was always present in the same altitudinal zone (Imbabura: *Steere 8203*, 15 December 1943). Since the original specimen, upon which Standley (1931) based *Cephaëlis Jamesonii*, was collected by Jameson "in declivitate occidentali montis Pichincha, alt. 2400 meters," it was considered worth while to search for *Cinchona pitayensis* there, in view of the common association of these two species in the more northern provinces. Consequently, a trustworthy field assistant and "conocedor," Antonio Romo, who had worked with me in Carchi and Imbabura, and who knew *Cinchona pitayensis* in the field, was entrusted with an independent

search for it on the west side of Pichincha. He worked south from Calacalí, and on May 24, on the Cerro de Campana, he found the first *C. pitayensis* collected south of the equator, a convincing corroboration of the theory outlined above. Since then, further survey work has shown a considerable quantity of this high-yielding species to exist on the slopes of Pichincha.

The discovery of *Cinchona pitayensis* on Pichincha demonstrated that this species had been able to migrate southward beyond a second phytogeographical barrier, the deep, desert valley of the Río Guayllabamba, and that it should occur still farther south. Consequently, further explorations were gotten under way at once in the western Andes between the volcanos Iliniza and El Corazón. *Cinchona pitayensis* was soon found to be abundant in the Province of León; north of Pilaló by G. W. Prescott, and in the region of Sigchos by M. Acosta-Solís. A curious feature of the species in León Province is that although its morphological character and its habitat preference are quite typical, its bark is not particularly rich in alkaloids, especially quinine. The cause of this unusual condition will probably be found in some soil factor, although the species itself may be more variable at the edge of its geographic range.

We continually heard rumors that a good quality of *Cinchona* was harvested by Colombians, in the last century, on the eastern slopes of the great mountain mass of Cayambe, in the Eastern Andes. In the hope that a new area of *Cinchona pitayensis* might be discovered, W. B. Drew, Ira L. Wiggins, and G. W. Prescott carried on extensive explorations under the most arduous and difficult field conditions imaginable, but without success. Nevertheless, this species probably does extend still farther south in both ranges of the Andes. The exploratory work, and any work of exploitation which may follow it, will always be made difficult by several factors, especially the cold, wet climate preferred by *Cinchona pitayensis*, the extreme ruggedness of the country and the consequent lack of trails between 2500 m. and 3500 m., and the unwillingness of the people to believe that high-yielding cascarilla can be obtained at such high altitudes (Steere 1944).

Cinchona pitayensis was proposed in 1849 by Weddell, not as a new species, but as a new name to replace *C. lanceolata* Benth. (1845), preoccupied by *C. lanceolata* Ruiz & Pavón (1799). Weddell chose the specific name "pitayensis" because the type specimen came from the region of Pitayó, as already mentioned. In Colombia, this species may form large trees, up to a meter in diameter (Karsten 1858; Standley 1930), and I have seen trees 80 cm. in diameter above Tacueyó, not far from the type locality. In Ecuador, the trees are smaller, and of hundreds of trees which I have seen, none had a trunk over 50 cm. in diameter, with an average of perhaps 35 cm. Furthermore, the leaves are more pubescent, especially when young, and the capsules are less strongly ribbed. The Ecuadorian form was pro-

posed as a new species, *Cinchona corymbosa*, by Karsten (1858), on the basis of specimens from southernmost Colombia. Although this name has generally been treated as a synonym of *C. pitayensis* (Standley 1930), there appears to me to be some reason to keep them separate, perhaps with varietal rank, especially after having seen both forms in the field. The abundant herbarium material which has been collected in Colombia and Ecuador during the past two years will eventually provide a definite answer to this problem, when the specimens can be gotten together for botanical study.

The form of *Cinchona pitayensis* which we now know to occur in the four northern Andean provinces of Ecuador is a beautiful tree with straight, unbranched trunk, which is clear white above and brown below. The white coloration, which is especially conspicuous in dry situations, apparently results from a growth of lichens. When the bark dries, it shows characteristic transverse fissures, especially bark from the upper part of the trunk. Because of its high alkaloid content, of which about half is quinine, the bark is very bitter with the peculiar taste of quinine, either fresh or dry. There are other members of the Rubiaceae which grow with *Cinchona pitayensis* and might be confused with it, but the very bitter bark of the *Cinchona* easily distinguishes it from other members of the family which occur at the same altitude. The rather slender trunk averages 30–35 cm. in diameter in mature trees, at breast height, and a tree of this size will give about 130 pounds of wet bark, if branches down to 6–7 cm. in diameter are stripped. Since the bark of *C. pitayensis* contains less water, on a percentage basis, than the bark of *C. pubescens*, we estimated in our survey work that three trees would produce one hundredweight of dry bark. The trunk does not branch until the crown is reached, and then suddenly breaks up into a complex system of stiff branches. The crown is conspicuously rounded, or often somewhat flat-topped. The leathery leaves are rather stiffly erect-spreading, clustered at the tips of the twigs, with a very characteristic aspect. When young they are a clear, dark green, and very glossy above. Some of the old leaves, especially when exposed to sunlight, become a bright scarlet before they fall off. When one examines the top of the forest from above or on the opposite side of a steep valley, this species can be recognized for a considerable distance by the rounded crowns, the deep green color and glossiness of the leaves, as well as their peculiar arrangement and the occasional scarlet old leaves. The trees usually occur in diffuse groups or manchas of 5–50, and are often more or less of the same size and age within the group. *Cinchona pitayensis* nearly always grows on very steep slopes, in regions with a heavy rainfall, and at altitudes between 2500 and 3230 m. Nearly every region in which this species occurs is decidedly volcanic, and it seems to reach its greatest abundance on the actual slopes of volcanos, from the Nevado del Huila in Colombia to El

Corazón in Ecuador. This species seems to inhabit only virgin forests and does not reappear if the forest is cut or burned, at least for a long time. The habit of *Cinchona pubescens* is very different, as it can colonize river bottoms, pasture fields, and abandoned clearings with the greatest facility.

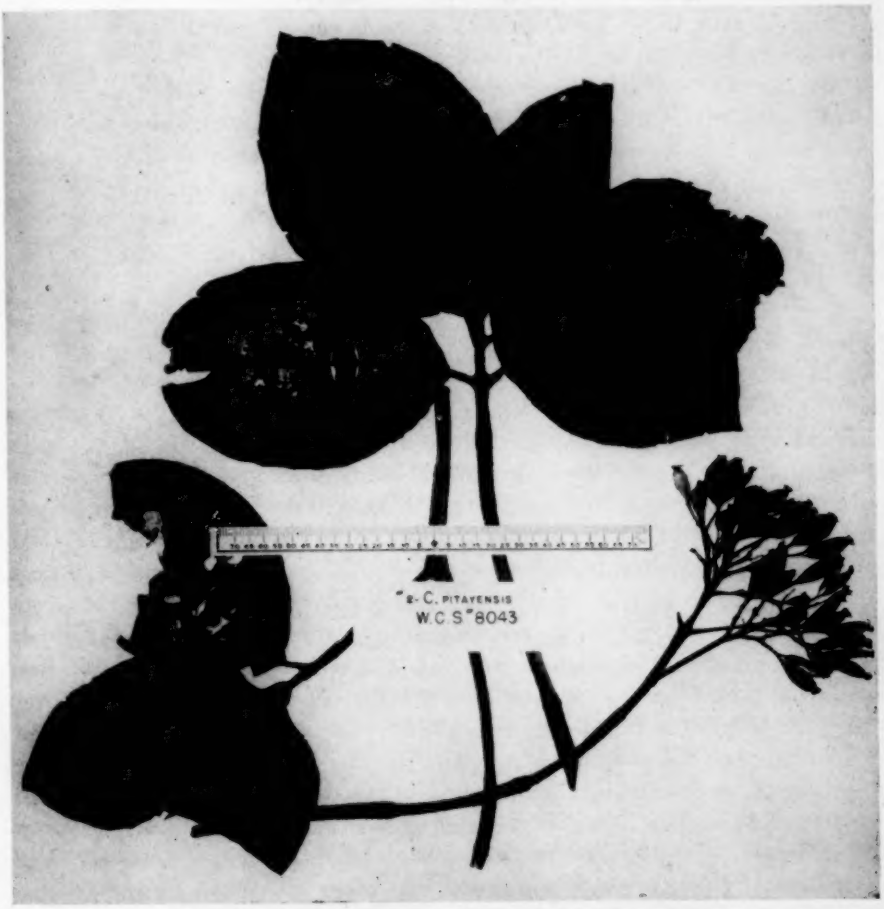

FIG. 1. *Cinchona pitayensis*, leaves and capsules. In this species some capsules dehisce at the base, and others at the apex. Photograph by courtesy of the Corporación Ecuatoriana de Fomento.

The flowers of *Cinchona pitayensis* in Eucador are brownish-purple to purple and have a strong fragrance of vanilla (coumarin). The inflorescence is very compact, and usually flat-topped, very different from the diffuse, elongated inflorescences of *C. officinalis* and *C. pubescens*. In the latter species, an inflorescence may reach a meter in length. The fruits, likewise, are in a compact, flat-topped cluster, and present a contradictory

condition in the genus *Cinchona*, since about as many of them open at the top and split downward as open at the bottom and split upward (fig. 1). Thus, in the same cluster of fruits one finds capsules opening in the typical *Cinchona* manner and others opening in the manner of *Remijia* or *Ladenbergia*. However, in view of the typical *Cinchona* flowers, and the high alkaloid content of the bark, as well as the group of alkaloids represented, there can be no doubt about the generic position of this species.

The vegetation of the *Cinchona pitayensis* forest is the typically luxuriant growth of a high altitude, broad-leaf rain forest. A commonly associated plant in the Cordillera Occidental is a climbing bamboo (*Chusquea scandens*), and in the Cordillera Oriental may be an enormous, broad-leaved grass (unidentified), locally called "chamizo." As already mentioned, a very useful indicator plant of proper altitude and habitat conditions for *Cinchona pitayensis* is *Cephaëlis Jamesonii*.

Soon after its original discovery in Colombia, *Cinchona pitayensis* was found to have the highest-yielding bark of any species in the country, not only in total alkaloids but also in quinine, and large quantities were harvested and exported under the name "quina de Pitayó." In the zone of Tacueyó, near the type locality on the west slope of the Nevado del Huila, the bark averages six per cent of total crystallizable alkaloids and three per cent of quinine sulfate. One of my samples gave the extraordinarily high analysis (for a wild bark) of 5.3 per cent of quinine sulfate and 8.1 per cent of total crystallizable alkaloids. In Ecuador, the alkaloid content of this bark does not seem to be so high as in the northern part of its geographic range, in Colombia, and it apparently becomes progressively less rich in alkaloids toward the south. The highest analysis I have seen for an Ecuadorian sample has been 7 per cent of total crystallizable alkaloids and very little over 4 per cent of quinine sulfate, whereas the average content is about 5 per cent of alkaloids and 2.5 per cent of quinine sulfate. Although this may not be quite as high as the alkaloid content of another form of *Cinchona pitayensis* in parts of Colombia, it still is the highest yield of any species in Ecuador, and is especially important because of its high consistency. An additional advantage of *Cinchona pitayensis* over the other Ecuadorian (and Colombian) species is that it produces the rare alkaloid quinidine in small but appreciable quantities (to 1 per cent). Quinidine is an essential drug for the treatment of certain heart diseases and does not exist as more than traces in any other *Cinchona* species of the northern Andes.

There is a strong and widespread feeling among Ecuadorian cascarilla producers that barks from lower altitudes are apt to be of a higher quality than barks from high altitudes. There is a certain amount of botanical evidence to support this idea, and it is obvious that plants will grow faster in the tropics at lower altitudes, other conditions remaining equal, because

of the increase in temperature. For example, in the western Andes, in the Province of Bolívar, the "serrana" variety of *Cinchona pubescens,* typical of high altitudes, contains an average of perhaps 3 per cent of pure cinchonine, without quinine or other alkaloids, whereas the "roja" variety of the same species, at much lower altitudes, produces bark with 4–5 per cent of total crystallizable alkaloids and 1–2 per cent of quinine sulfate. In the Eastern Andes, the variety of *Cinchona officinalis* which occurs in the valley of the Río Pastaza between 1200 m. and 1500 m. produces bark with an average of four per cent of total crystallizable alkaloids and one per cent of quinine sulfate. On the other hand, the variety which occurs at about 2000 m. produces bark with less than two per cent of total alkaloids and no quinine, so that it is economically worthless. One of the most interesting experiments that could be performed in Ecuador would be to plant seedlings or cuttings of *Cinchona pitayensis* of a high-yielding clone at different altitudes, in order to see if the quinine sulfate content could be increased by altering the climatic factors. Under any circumstance, this species is one of the many rich botanical resources of Ecuador, and is worthy of extensive experimental study, which will undoubtedly result in the development of valuable cultivated varieties.

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SOME MELASTOMACEAE OF COLOMBIA

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The recent intensive collecting of Dr. José Cuatrecasas in various parts of Colombia has yielded many interesting species of Melastomaceae, including several novelties and several others hitherto unknown to Colombia, at least so far as my records indicate. Those in the genera *Blakea* and *Topobea* have already been discussed in a separate paper.

Excluding these two genera, 93 species have been identified, of which 15 appear to be undescribed. This would be a very high proportion if the plants had come from the Andes. Most of them were collected in the coastal region of El Valle, which has been neglected by most botanical explorers and which yielded numerous new species to Triana many years ago. Several of his plants were re-collected, probably for the first time. There are still a number of specimens unidentified, chiefly because of lack of flowers, without which genera of this family can seldom be determined with assurance. Among them there appear to be the little known *Miconia caelata* (Bonpl.) DC., a new *Miconia* related to *M. parvifolia* Cogn., a new *Henriettella*, and probably some other undescribed species.

Ptilanthus Gleason, gen nov. Hypanthium hemisphaericum anguste 5-alatum, inter alas 5-nervium. Calycis tubus non productus; sepala triangularia secus medium alata, dentibus exterioribus nullis. Petala lanceolata angustissime acuminata. Stamina 10 isomorpha; antherae subulatae poro terminali dehiscentes; connectivum infra thecas brevissime productum exappendiculatum. Ovarium multiovulatum liberum summo tomentulosum; stylus rectus gracilis; stigma punctiforme. Inflorescentia terminalis paniculiformis.

Ptilanthus scandens Gleason, sp. nov. Liana magna, ramis ultimis subteretibus arcte furfuraceis. Petioli graciles, 2–4 cm. longi, dense brunneofurfuracei. Laminae herbaceae, late ovatae, 8–14 cm. longae 6–10 cm. latae, apice subiter contractae in apiculum obtusum 1–2 cm. longum, basi leviter cordatae lobis paulo productis et saepe revolutis, supra glabrae, subtus ad venas furfuraceae ad paginam minutissime brunneo-punctatae, 5-pli-nerviae jugo uno marginali altero submarginali neglecto. Cyma paniculiformis terminalis ca. 5 cm. longa. Flores 5-meri brevissime (usque 1 mm.) pedicellati. Hypanthium glabrum 2.2 mm. longum. Sepala 0.9 mm. longa acuta. Petala alba 6 mm. longa, longe acuminata. Filamenta complanata 2.2 mm. longa; antherae 2.6 mm. longae, poro ventro-terminali dehiscentes. Ovarium 3-loculare; stylus 3 mm. longus.

TYPE: *Cuatrecasas 15807*, from the Pacific coast of El Valle, Colombia, alt. 5–50 m. Since fruit is lacking, it is impossible to decide to which tribe of the Melastomaceae the plant belongs. It is a fact that a superior ovary,

such as our plant exhibits, is usually followed by a capsular fruit and an inferior ovary by a baccate fruit, but there are exceptions in both cases. Every character enumerated in the generic characterization can be duplicated separately in some other genus, but the combination of all gives this plant a structure not matched in any genus of the family, so far as it is known to me.

Calyptrella littoralis Gleason, sp. nov. Liana, teste cl. Cuatrecasas. Caules minores dense lepidoto-furfuracei demum glabrescentes. Petioli 8–15 mm. longi. Laminae subcoriaceae, ovato-oblongae vel ovato-lanceolatae, usque ad 10.5 cm. longae 5 cm. latae, caudato-acuminatae ad apicem obtusum, integrae, basi rotundatae vel leviter cordulatae, 5-nerviae jugo exteriore submarginali, supra primum minutissime lepidotae, utrinque densiuscule resinoso-punctatae. Panicula terminalis pauci-ramosa 6 cm. longa furfuracea. Flores 4-meri in capitulis paucifloris ramulos terminantes. Hypanthium poculiforme, 3.5 mm. longum, arete minuteque lepidotum. Calyx calyptriformis lepidotus ad torum deciduus. Petala alba obovata acuta 4 mm. longa. Stamina isomorpha; filamenta 2.6 mm. longa; antherae linearisubulatae, poro ventro-terminali dehiscentes, thecis convolutis 2.6 mm. longis; connectivum non elevatum, infra thecas 2 mm. productum quasimodo *Graffenrieda*. Ovarium superum, 2(?)-loculare; stylus 4 mm. longus; stigma punctiforme.

TYPE: *Cuatrecasas 17698*, collected at Quebrada de Guapecito, alt. 0–5 m., on the coast of El Valle. A typical *Calyptrella* in every respect except its climbing habit. Three other 4-merous species of the genus have been described, of which *C. robusta* Cogn. has large 7-nerved leaves, *C. tristis* Triana has coriaceous leaves obtuse or acute at base, and *C. gracilis* Triana has thin leaves cuneate at base. The two latter species have much smaller flowers than *C. littoralis* and lack the resin-dots on the leaves. All three grow at fairly high elevations in the Andes.

Conostegia rubiginosa Gleason, sp. nov. Arbor. Caules, petioli, venae subtus, inflorescentia, et hypanthia dense rubiginoso-tomentosa, pilis crassis barbellatis et partim stellatis. Petioli 1–2 cm. longi. Laminae subcoriaceae, anguste obovato-oblongae, usque ad 20 cm. longae 9 cm. latae, abrupte caudato-acuminatae, acumine 1–2 cm. longo, integrae, basi obtusae, 5-nerviae vel sub-5-pli-nerviae, supra glabrae opacae, subtus stellato-pubescentes, supra venis planis secundariis obscuris, subtus venis omnibus valde prominentibus. Inflorescentia ca. 10 cm. longa. Alabastra acuta, obovoidea, 10 mm. longa. Hypanthium hemisphaericum, ca. 5 mm. longum. Petala alba, late triangulari-obovata, 9 mm. longa, fere totidem lata, multinervia, uno latere erosa. Stamina 24 isomorpha. Filamenta 3.3–3.5 mm. longa. Antherae oblongae, obtusae, 2.7 mm. longae, thecis infra filamentum breviter productis; connectivum simplex. Stylus teres, 5.6 mm. longus; stigma capitatum, fere 1 mm. latum.

TYPE: *Cuatrecasas 17700*, collected at Quebrada de Guapecito, Pacific coast of El Valle, alt. 0–5 m.; also *17538*, from the same region. The species differs from other Colombian representatives of the genus in its densely tomentose stems and inflorescence.

Conostegia Cuatrecasii Gleason, sp. nov. Frutex vel arbor parva usque ad 4 m. alta. Caules, petioli, rami quadrangulati, et inflorescentiae tenuiter

stellato-furfuracea. Petioli usque ad 4 cm. longi. Laminae tenues, ellipticae, usque ad 24 cm. longae 11 cm. latae, abrupte angustatae in apiculum obtusum ca. 1 cm. longum, basi acutae, obtusae vel subrotundae, 5-pli-nerviae, supra glabrae nitentes, subtus glabrae opacae. Panicula pyramidalis, longe pedunculata, 5–13 cm. longa. Alabastra obovoidea, 8–9 mm. longa, acuta, breviter apiculata, glabra, rugulosa. Flores 6-meri. Hypanthium hemisphericum, 3.7 mm. longum. Petala alba vel rosea, valde inequilatera, obovata, 9–10 mm. longa. Stamina isomorpha. Filamenta loricata 5 mm. longa. Antherae oblongae, obtusae, 3.5–4 mm. longae, poro terminali dehiscentes, 4-loculare; thecis cum connectivo infra apicem filamenti breviter productis in lobos 2 rotundatos. Ovarium inferum, 6-loculare. Stylus 5.5 mm. longus, superne paullo dilatatus; stigma capitatum, 1.3 mm. latum.

TYPE: *Cuatrecasas 17612*, collected on the Río Cajambre, coast of El Valle, alt. 5–80 m.; other specimens collected by him in the same general locality are *14386*, *17001*, *17273*, and *15142*, the latter at an altitude of 900–1180 m. Another sheet is *Killip 11805*, from the Río Dagua, which, according to my notes of 1928, is the same as *Triana 3942*. It is closely related to *C. Poeppigii* Cogn., in which the buds are only 7 mm. long or less, the petals pink, 6 mm. long and proportionately much wider, the stamens smaller, and the style shorter.

Miconia calcarata Gleason, sp. nov. Arbor grandis, ramis ultimis teretibus obscure brunneo-furfuraceis mox glabris. Petioli ca. 1 cm. longi, supra canaliculati, glabri. Laminae subcoriaceae late ellipticae usque ad 13 cm. longae 8.5 cm. latae, abrupte breviterque accuminatae, basi abrupte lateque cuneatae, juventute utrinque minutissime lepidotae maturitate fere glabrae, 5-nerviae, venis secundariis sub angulo ca. 70° adscendentibus, 5–10 mm. distantibus. Inflorescentia paniculiformis pedunculata 5 cm. longa; pedicelli 3–6 mm. longi. Hypanthium campanulatum 3.7 mm. longum, minute furfuraceum. Calycis tubus erectus 0.8 mm. longus; lobi suberecti a sinibus acutis, late ovati, subacuti, 0.6 mm. longi. Petala triangulari-ovata alba, 2.8 mm. longa, breviter unguiculata, basi truncata, subacuta. Stamina 10 dimorpha; filamenta jam non matura; antherae breviores lineares 3.1 mm. longae, obtusae, 4-loculares, facile fissiles, connectivo basi paullo incrassato in lobos 3 rotundatos laterales; antherae longiores lineares 4.5 mm. longae, apice complanatae, 4-loculares, connectivo basi breviter producto, diviso in lobos 2 laterales teretes lineares deflexo-curvatos 1.5 mm. longos. Ovarium fere superum, 3(?)-loculare; stylus validus teres 6.5 mm. longus; stigma truncatum.

TYPE: *Cuatrecasas 17702*, collected at Quebrada de Guapecito, Dept. El Valle, alt. 0–5 m. The species can not be assigned satisfactorily to any section of *Miconia*. Four-celled anthers are known to me only in the section *Amblyarrhena* and a few species of *Cremanium;* in all of these the anthers are short and broad and open by a single pore. The pore was not definitely seen in our plant, but there are obviously two of them. Among hundreds of species of *Miconia* which I have carefully examined, petals and connective of this character have never been noted. However, the plant has in every way the general facies of a *Miconia*. If it is excluded from the genus, the problem of placing it elsewhere arises, and I know of no other genus to which it can be referred without doing violence to existing generic concepts.

Miconia blakeaefolia Gleason, sp. nov. (Sect. *Tamonea*). Liana magna, teste el. Cuatrecasio. Caules juveniles obscure obtuseque quadrangulati, petioli, et inflorescentia minute brunneo-puberula. Petioli 6–10 mm. longi. Laminae coriaceae, violaceo-suffusae, ellipticae, usque ad 11 cm. longae 4.5 cm. latae, abrupte acuminatae, acumine saepe recurvo vel torto, integrae, basi rotundatae, 5-pli-nerviae, jugo exteriori submarginali, supra glabrae subnitentes, subtus ad paginam glabrae ad venas puberulae; venae secundariae 1.5 mm. distantes transversae. Panicula 8–12 cm. longa. Flores 5-meri sessiles. Hypanthium tubulosum, 3.6 mm. longum, glabrum. Calycis tubus erectus, 1 mm. longus; sepala fere semicircularia, 1 mm. longa a sinibus acutis, minutissime ciliata. Petala rubro-violacea, oblonga, 6–7 mm. longa, ca. 3 mm. lata. Stamina isomorpha. Filamenta gracilia, glabra, 3.8 mm. longa. Antherae anguste subulatae, valde arcuatae, 4.6 mm. longae, 2-loculares; connectivum simplex. Ovarium inferum, 5-loculare; stylus glaber, crassus, 5 mm. longus, summo curvatus; stigma capitatum, 0.8 mm. latum.

TYPE: *Cuatrecasas 15181*, collected at Piedra de Moler, on the western slope of the Cordillera Occidental, Dept. El Valle, alt. 900–1180 m.; *14924*, from the same locality, is identical. See discussion under *M. transversa*.

Miconia transversa Gleason, sp. nov. (Sect. Tamonea). Arbor 10 m. alta, ubique glabra. Caules subteretes. Petioli 6–12 mm. longi. Laminae coriaceae, virides, oblongo-ellipticae, usque ad 15 cm. longae 5.5 cm. latae, abrupte acuminatae, acumine 8–10 mm. longo, integrae, basi longe cuneatae, 5-pli-nerviae; venae secundariae transversae, 1.5–2 mm. distantes. Panicula ramosa, ca. 12 cm. longa. Flores sessiles, 5-meri. Hypanthium tubulosum, 3 mm. longum. Calycis tubus erectus, fere 0.5 mm. longus, truncatus, minutissime ciliatus. Petala rosea, oblonga, 5.2 mm. longa, 2 mm. lata. Stamina isomorpha. Filamenta gracilia, 3 mm. longa. Antherae anguste subulatae, valde arcuatae, ca. 5 mm. longae, 2-loculares; connectivum simplex. Ovarium inferum 3(?)-loculare; stylus glaber, crassus, 4.5 mm. longus, summo curvatus; stigma capitatum, 1 mm. latum.

TYPE: *Cuatrecasas 17459*, collected at Silva, on the Pacific coast of Dept. El Valle, alt. 5–80 m.; *17488A*, from the same place, is identical.

The only species with which this and *M. blakeaefolia* might be confused is the mysterious *M. foliosa* Triana, not seen by Cogniaux, not found by me in European herbaria, not photographed by Macbride. One clause of Triana's description, "calycis . . . limbo . . . obtuse 4?-lobo," may suggest that he had very scanty material. Our *M. blakeaefolia* differs from Triana's description in its pubescence and its leaves rounded at base; *M. transversa* differs in its truncate calyx; both differ in their slender petioles and distinctly pli-nerved leaves.

Miconia centronioides Gleason, sp. nov. (Sect. *Adenodesma*). Arbor magna, ramis ultimis, petiolis, pagina foliorum inferiori, inflorescentia, hypanthiis, calycibus arctissime cinereo-stellato-lepidotis. Petioli validi 2–3 cm. longi. Laminae firmae anguste obovatae, usque ad 15 cm. longae 7 cm. latae, superne rotundatae ad apiculum parvum triangularem, basi cuneatae, superne glabrae lucidae, 3-nerviae, jugo marginale neglecto. Inflorescentia terminalis brachiata ca. 2 dm. longa, ramis arcte adscendentibus. Flores numerosi breviter pedicellati 5-meri. Hypanthium hemisphaericum 3 mm. altum, supra ovarium valde inerassatum ovarium fere obtegens, toro ergo

centrali. Calyx 3 mm. longum exacte truncatum paulo ampliatum, dentibus externis 5 minutis notatum. Petala rosea obovato-oblonga 19 mm. longa 12 mm. lata, superne rotundata, extus cinereo-lepidota. Stamina fere isomorpha. Filamenta glabra 9.5 mm. longa. Antherae subulatae 6.7 mm. longae, thecis in parte inferiore valde convolutis superne rectis attenuatis ad porum ventro-terminalem. Connectivum prope basin incrassatum canaliculatum circum bases thecarum curvatum et incrassatum densiuscule glandulosum. Ovarium 5-loculare; stylus sigmoideus glaber 14 mm. longus; stigma peltatum 2.3 mm. diam.

TYPE: *Cuatrecasas 14145*, collected on the Rio Micay, Dept. Cauca, alt. 5–20 m. *Cuatrecasas 17676*, from Quebrada de Guapecito, Dept. del Valle, alt. 0–5 m. is conspecific; its leaves are up to 22 by 10 cm. and the calyx is 4 mm. long. The glandular subulate anthers place it in the section *Adenodesma;* its greatly thickened hypanthium associates it with *M. axinaeoides* Gl. and *M. megalantha* Gl. The latter is especially similar to *M. centronioides*, but is distinguished by its larger leaves nearly glabrous beneath, glandular filaments and style, slightly dimorphic anthers, and ovary with flaring summit.

Miconia platypoda Gleason, sp. nov. (Sect. *Eumiconia, Diplostachyeae*). Frutex, caulibus arcte brunneo-stellato-tomentosulis atque petiolis et inflorescentiis, pilis sessilibus multiradiatis. Petioli 10–18 mm. longi valde lateraliter compressi. Laminae anguste elliptico-oblongae, usque ad 18 cm. longae 5 cm. latae, acuminatae, integrae, basi cuneatae, 3-pli-nerviae, jugo marginali obscuro neglecto, juveniles utrinque sparse stellatae, mox glabrescentes. Spicae 3, 5–10 cm. longae; flores 4-meri sessiles, solitarii vel bini. Hypanthium ellipsoideum, 2.4 mm. longum, sparse griseo-stellatum. Calycis tubus 0.4 mm. altus; sepala triangularia, a toro 1.1 mm. longa. Petala alba, obovata, 1 mm. longa, erecta. Stamina isomorpha. Filamenta gracilia, 1.2 mm. longa. Antherae anguste lineares, 1.8 mm. longae, 2-loculares. Connectivum infra thecas 0.2 mm. productum in lobos 2 laterales. Ovarium semiinferum, glabrum; stylus cylindricus, 4.3 mm. longus; stigma truncatum.

TYPE: *Cuatrecasas 7185*, collected at Cerro de Circasia, Vaupés, alt. 300–500 m. We have here the first known relative of *M. marginata* Triana, which has a similar inflorescence, petals, stamens, and stigma. In it the foliage and hypanthium are glabrous, the lateral nerves of the leaf are strictly marginal, and the margin of the leaf is peculiarly reflexed.

Miconia gracilis Tr. No. 17338 apparently represents this species, which I have not previously noted from South America.

Miconia stipitata Gleason, sp. nov. (Sect. *Eumiconia, Glomeratiflorae*). Frutex 2–3 m. altus, caulibus dense hirsutis, pilis stipitato-stellatis. Petioli 5–10 mm. longi, stipitato-stellati. Laminae tenues, anguste ovato-lanceolatae, acuminatae, integrae, basi cordatae, 3-nerviae, jugo marginali neglecto, utrinque stipitato-stellatae. Panicula ramosa; flores sessiles 5-meri ad apicem ramulorum. Hypanthium anguste campanulatum, 2 mm. longum, stipitato-stellatum. Calycis tubus 0.4 mm. productus; sepala depresso-triangularia e sinibus acutis, a toro 1 mm. longa; dentes exteriores crasse subulati, pubescentes, sepala 0.4 mm. excedentes. Petala alba, oblonga, ca. 3 mm. longa, inaequaliter retusa. Stamina dimorpha. Filamenta gracilia. Antherae lineares, 3 vel 2.3 mm. longae, 2-loculares, poro terminali. Connectivum infra thecas 0.5 mm. productum, in ser. ext. basi truncatum, lateraliter

expansum in lobos 2 deflexos margine pauci-glandulosos, in ser. int. in lobos 2 laterales eglandulosos divisum. Ovarium semi-inferum, 3-loculare, summo glabrum; stylus rectus, teres, 4.6 mm. longus; stigma truncatum.

TYPE: *Cuatrecasas 13713*, collected at Quebrada del Cauchal, western slope of the Cordillera Occidental, Dept. El Valle, alt. 300 m. The stalk of the stellate hairs is about 1 mm. long on the stem, petioles, veins, and inflorescence, 0.5 mm. on the leaf-surface, and still shorter on the hypanthium. Pubescence of this type is relatively uncommon in *Miconia*, where it is particularly characteristic of *M. barbinervis* (Benth.) Tr., *M. stelligera* Cogn., and *M. clavistila* Gl. Our plant differs from all of these in its dimorphic glandular stamens; in the first of the three the leaves have simple bristles on the upper side and in the other two they are essentially glabrous.

MICONIA LANATA (DC.) Tr. *16969*. A species of Guiana and the Amazonian lowlands, not heretofore seen by me from Colombia.

MICONIA COMPACTA Gleason (1931; *M. semota* Markg. 1934). Originally described from Iquitos, Peru, the species now appears in the Vaupés region of southeastern Colombia (*6939*).

MICONIA RUFICALYX Gleason. Heretofore known only from British Guiana (*16745*).

MICONIA PILGERIANA Ule. A fairly well known species of the lowlands of the upper Amazon valley which now appears in southwestern Colombia (*16907*). It was assigned by its author to section *Cremanium* and in 1931 I suggested that it belonged better with section *Glossocentrum* because of the wide terminal pore of the anthers. The anthers at full maturity extend this pore into two longitudinal clefts, a character of section *Chaenanthera*, and very closely resemble those of the Andean *M. dolichorrhyncha* Naud.

Clidemia vallicola Gleason, sp. nov. (Sect. *Staphidium*). Frutex vel arbuscula ramosa, ramis ultimis dense stellato-tomentosis atque glanduloso-hirsutis, pilis 0.5–1.5 mm. longis. Petioli validi 1–2 cm. longi, stellato-tomentosi et densissime hirsuti. Laminae tenues, late ovatae, usque 18 cm. longae 14 cm. latae, abrupte acuminatae, fere integrae, basi cordatae, 5–7-nerviae, supra minute glandulosae, pilis 0.2 mm. longis, subtus ad paginam sparse glandulosae, pilis 0.1 mm. longis, ad venas glanduloso-setosae. Inflorescentiae axillares paniculiformes, ramis paucis ultra medium paucifloris. Flores 7-meri. Hypanthium campanulatum supra ovarium constrictum 4 mm. longum, dense glanduloso-hirsutum. Calycis hirsuti tubus 1 mm. longus, lobi ovati a toro 2.3 mm. longi; dentes exteriores adnati, sepala 1 mm. excedentes, dense hirsuti. Petala obovato-oblonga 7 mm. longa. Stamina numerosa (22 enumerata) isomorpha; filamenta gracilia 4 mm. longa; antherae subulatae 2.7 mm. longae, poro dorso-terminali dehiscentes; connectivum infra thecas breviter productum et incrassatum. Ovarium 7-loculare inferum, apice minutissime glanduloso-setulosum; stylus 7 mm. longus; stigma truncatum.

TYPE: *Cuatrecasas 13735*, collected at Quebrada del Danubio, Dept. El Valle, alt. 300–350 m.; *Cuatrecasas 14401* is the same; also on the coast of El Valle, *Cuatrecasas 13998*. The nature of the inflorescence, the structure of the stamens, and the character of the pubescence show its close relationship to *C. novemnervia* (DC.) Triana. Our plant differs in its 7-merous flowers, its numerous stamens, and the pubescence of the leaves.

Clidemia crenulata Gleason, sp. nov. (Sect. *Sagraea*). Frutex 2 m. altus, ramis teretibus dense breviterque hirsutis, pilis glandulosis ca. 2 mm. longis. Formicaria hirsuta, persistentia ad basim petioli. Petioli hirsuti usque ad 5 cm. longi. Laminae tenues ovato-oblongae usque ad 25 cm. longae 14 cm. latae, breviter caudato-acuminatae, insigniter crenulatae, basi rotundatae paullo emarginatae, 5-nerviae, jugo submarginali neglecto, utrinque sparse hirsutae. Inflorescentiae axillares multiflorae congestae. Flores sessiles 4-meri. Hypanthium tubuloso-urceolatum 4.7 mm. longum infra medium sparse glanduloso-hirsutum. Calycis tubus 0.2–0.3 mm. productus erectus; lobi depressi late rotundati; dentes exteriores subapicales patuli 0.6–0.9 mm. longi. Petala oblonga obtusa 3.7 mm. longa. Stamina isomorpha; filamenta 3.7–4 mm. longa; antherae subulatae 4.7 mm. longae, poro apicali dehiscentes; connectivum simplex. Ovarium 4-loculare inferum; stylus gracilis glaber 11 mm. longus; stigma capitatum.

TYPE: *Cuatrecasas 16534*, collected at La Trojita, Dept. El Valle, alt. 5–50 m. It is obviously related to *C. petiolata* (Rich.) DC., differing in the pubescence of the petiole and lower leaf-surface as well as in the presence of formicaria which are persistent after the leaves have fallen.

CLIDEMIA RAMIFLORA Gleason var. **colombiana** Gleason, var. nov. Frutex 1–2 m. altus, caulibus juvenilibus cum petiolis 4–6 cm. longis dense stellato-furfuraceis fere velutinis. Cymae infra folia orientes, pluriflorae trichotomae ramosae 2–4 cm. longae. Flores 4-meri. Sepala, petala, et stamina deficientes. Laminae ovatae, usque ad 23 cm. longae 15 cm. latae, abrupte acuminate in apicem obtusum, minute serrulatae, basi late rotundatae et cordulatae, 7-nerviae, utrinque glabra praeter venas majores stellato-furfuraceas.

TYPE: *Cuatrecasas 17298*, collected at San Isidro, Dept. del Valle, alt. 5–100 m. Its assignment to *C. ramiflora* is based solely on superficial resemblance. The type differs in a closer and finer pubescence and in leaves elliptic rather than ovate.

Clidemia panamensis (Blake & Standley) Gleason, comb. nov. *Prosanerpis panamensis* Blake & Standley, Field Mus. Publ. Bot. **4**: 245. 1929; *C. epiphytica*, in part, Gleason, Brittonia **3**: 131. 1939. I combined the two species under the earlier name because of close similarity in foliage and calyx. More material shows that the two are distinct, the hypanthium of *C. epiphyta* being nearly glabrous, while that of *C. panamensis* is distinctly hirsute.

Ossaea resinosa Gleason, sp. nov. Liana epiphytica lignosa, ramis gracilibus valde elongatis, minutissime brunneo-furfuraceis. Petioli 10–15 mm. longi. Laminae tenues opacae lanceolatae, usque ad 8 cm. longae 3 cm. latae, longe caudato-acuminatae, basi rotundatae, 3-nerviae jugo submarginali neglecto, ubique praesertim subtus resinoso-punctatae. Pedunculi axillares gracillimi, usque ad 4 cm. longi, saepissime 3-flori, bracteis 2 linearibus ca. 1 cm. longis, floribus 2 axillaribus subsessilibus, 1 terminali pedicellato. Flores 4-meri. Hypanthium cum calyce ellipsoideum 3.7 mm. longum, minutissime furfuraceum. Sepala conniventia (an semper?) minuta, dentibus exterioribus crasse subulatis 0.5 mm. longis. Petala jam immatura late triangularia acuta 1.5 mm. longa. Filamenta immatura; antherae lineares vel lanceolatae 2 mm. longae, poro ventro-terminali dehiscentes; connectivum infra thecas

angustatum 0.4 mm. productum in calcar conicum. Ovarium 3-loculare; stylus gracilis jam 1.4 mm. longus; stigma punctiforme.

TYPE: *Cuatrecasas 16619*, collected at La Trojita, Dept. del Valle, alt. 5–50 m. The immature condition of the flowers does not permit as full a description as desired, but its habit, inflorescence, and resinous indument are at variance with all other described species.

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JUNIPERUS VIRGINIANA, J. HORIZONTALIS, AND J. SCOPULORUM—V. TAXONOMIC TREATMENT

NORMAN C. FASSETT

These studies have been based on part or all the material in several herbaria: the Arnold Arboretum, the Gray Herbarium, the New York Botanical Garden, the University of Wisconsin, the University of Minnesota, Iowa State College, and North Dakota State Agricultural College. Herbarium material has been supplemented by mass collections from localities representing nearly the whole range of *J. virginiana*, much of the eastern part of the range of *J. scopulorum*, and a number of localities of *J. horizontalis*. The mass collections have consisted of a sample from each individual tree or shrub in a colony; by their use it has been possible to study not only individuals but populations, and to see how certain characters vary within certain small areas. Much of the collecting was made possible by grants from the Wisconsin Alumni Research Foundation.

With certain exceptions in the areas shown on Map 2, individuals of this group may be identified by the following key:

a. Leaves[1] overlapping, their epidermal cells 5–20 μ wide, averaging 9–12 μ, mostly 10 μ; not more than 33% of peduncles of female cones curved; cones maturing in one year, 2.0–6.5 mm., mostly 3.5–5.5 mm., long; nearly all seeds with shallow pits.

b. Trunks erect.

c. Height of crown 1–2 times its width. *J. virginiana.*

c. Height of crown 2.5–7.5 times its width. *J. virginiana* var. *crebra.*

b. Matted shrubs, with stems creeping or somewhat ascending. *J. virginiana* var. *ambigens.*

a. Leaves overlapping or not, their epidermal cells 5–35 μ wide, averaging 13–19 μ, mostly 15 μ; 8–100% of peduncles of female cones curved; cones mostly maturing in two years, 4–9 mm., mostly 5.5–6.5 mm., long, seeds pitted or not.

d. Leaves rarely overlapping and then but slightly, their tips blunt; foliar glands longer than the distance from the gland to the tip of the leaf; 8–70% of peduncles of female cones curved; seeds nearly all with deep pits about half the length of the seed; trees, or shrubs with ascending branches about 1 m. high.

e. Trees with erect or strongly ascending trunks.

f. Height of tree 1–2 times its width. *J. scopulorum.*

f. Height 2.5–3.0 times width. *J. scopulorum* var. *columnaris.*

e. Depressed shrubs. *J. scopulorum* var. *patens.*

[1] In each case the mature scale-like leaves are meant. Acicular leaves have the width of epidermal cells characteristic of the species, but do not show the differences in overlapping or in leaf tips. All the specific characters have been discussed in detail in paper I of this series, Bull. Torrey Club **71**: 410–418.

d. Leaves mostly overlapping, their tips apiculate; foliar glands shorter than the distance from the gland to the tip of the leaf; 60–100% of peduncles of female cones curved; about half the seeds with shallow pits less than half the length of the seed; prostrate matted shrubs.

J. horizontalis.

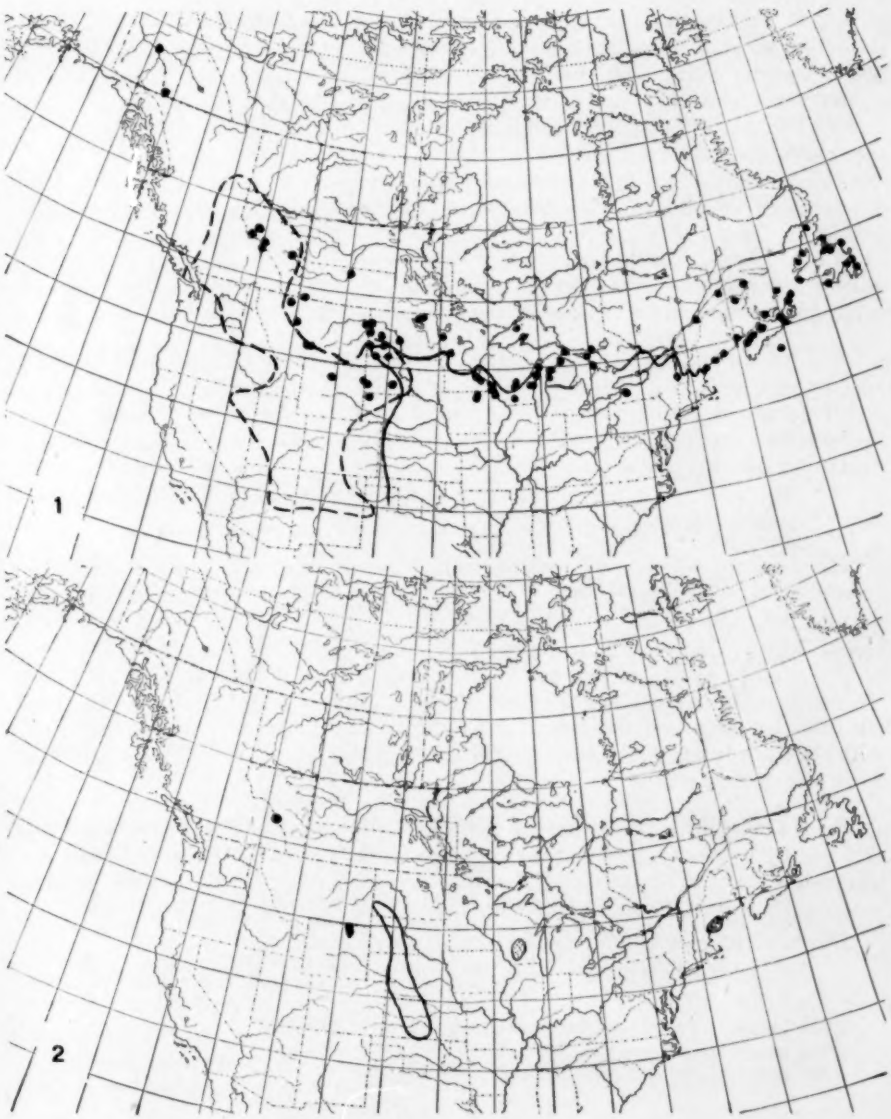

FIG. 1. Heavy solid line: approximately northern and western limits of *J. virginiana*. Heavy broken line: approximate limits of *J. scopulorum*. Dots: range of *J. horizontalis*. FIG. 2. Stippled areas: regions of probable crossing of *J. virginiana* and *J. horizontalis*—*J. virginiana* var. *ambigens*. Area enclosed by heavy line: region of hybrid swarms of *J. virginiana* and *J. scopulorum*. Solid black areas: localities for *J. scopulorum* var. *patens*.

1. J. VIRGINIANA L. Sp. Pl. 1039. 1753. Southern Maine, southern Ontario, southern Wisconsin and southwestern North Dakota, southward (fig. 1, heavy solid line). The southern limits are not determined, since the relation of this species to *J. silicicola* (Small) Bailey and *J. lucayana* Britton has not been studied.

1a. J. VIRGINIANA var. CREBRA Fernald & Griscom, Rhodora **37**: 133. 1935; description and range amended by Fassett, Am. Jour. Bot. **30**: 469–477. 1943. Locally replacing the typical form of the species in New England, eastern and central New York, New Jersey to western Virginia; northern Indiana to southeastern Wisconsin; southern Indiana; Knoxville, Tennessee; southern Missouri.

1b. J. VIRGINIANA var. AMBIGENS Fassett, Bull. Torrey Club **72**: 380. 1945. In areas of overlap of the range of *J. virginiana* with *J. horizontalis*, and probably the result of hybridization between these two species, on the coast of Maine from Lincoln County to York County. Although most individuals may be identified as this variety or as one of the purported parent species, some plants may show various other combinations of characters.[2]

2. J. SCOPULORUM Sargent, Gard. & For. **10**: 420. 1897. South Dakota to eastern Nevada and Vancouver Island, north into British Columbia and Alberta, south to northeastern Arizona and northwestern Texas (heavy broken line, fig. 1). Where the range overlaps or approaches that of *J. virginiana* (region enclosed by a heavy black line on figure 2), the characters of the two species occur in many recombinations,[3] and many individuals cannot be identified by the key.

2a. J. SCOPULORUM var. **columnaris** Fassett, var. nov. Arbor altitudine latudinen 2.5–3.0-ple. NORTH DAKOTA: bottom of deep gully, edge of pine region, Amidon, Slope County, May 15, 1941, *O. A. Stevens 504* (TYPE in Herb. North Dakota Agricultural College). Dr. Eltar Nielsen sends me a photograph of a similar tree at Spanish Point, near Williston, North Dakota.

2b. J. SCOPULORUM var. PATENS Fassett, Bull. Torrey Club **72**: 46. 1945. On the west slopes of the Big Horn Mountains, Wyoming, and about Banff, Alberta; doubtless elsewhere (solid black areas, fig. 2). Perhaps a hybrid with *J. horizontalis*.[4]

3. J. HORIZONTALIS Moench, Meth. 699. 1794. Locally from Newfoundland and southern Maine, westward along the Great Lakes; Wisconsin, Iowa and Minnesota to northwestern Nebraska and northern North Dakota to Montana; northwestward to Yukon Territory (dots, fig. 1).

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[2] See paper IV of this series, Bull. Torrey Club **72**: 379–384.
[3] See paper II of this series, Bull. Torrey Club **71**: 475–483.
[4] See paper III of this series, Bull. Torrey Club **72**: 42–46.

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PLANT TAXONOMY AND FLORISTICS

(exclusive of fungi)

(See also under Genetics, Goodwin)

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